BIOSYSTEMATICS OF THE YELLOW-FACED POCKET GOPHER, CRATOGEOMYS CASTANOPS (RODENTIA: GEOMYIDAE) IN THE UNITED STATES

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Introduction

The problem addressed herein is the systematic and evolutionary relationships, from a morphometric perspective, of currently recognized races of *Cratogeomys* in the United States. On the basis of published findings to the end of 1987, nine subspecies of *C. castanops* currently are recognized as occurring in the United States. Eight of these occur in Texas, with the possibility of the ninth occurring in the extreme northwestern corner of the Texas Panhandle. This species also occurs in Colorado, Kansas, New Mexico, and Oklahoma, and southward into México. Since Russell's (1968*b*) revision of the genus *Pappogeomys* (sensu lato), no taxonomic study has been done concerning more than two adjacent subspecies. Several criticisms of Russell's (1968*b*) work can be made: his analysis was not of a statistical nature; specimens from many intermediate geographic areas were not available to him, and, in fact, his study was based on relatively few specimens from the overall distribution of the species. Moreover, Russell (1968*b*) discussed two subspecies as ". . . occurring sympatrically with no apparent intergradation. . ." in the Guadalupe Mountains of Texas. Schmidly (1977) also reported two races from another locality in the Trans-Pecos region of Texas. Such situations likely do not exist unless more than one species is involved.

Historical Taxonomy

The genus *Cratogeomys*, which contains 10 species (Lee and Baker, 1987), occurs from southeastern Colorado south to southern México (Hall, 1981). The only species that occurs north of México is *C. castanops*. Baird (1852) described *castanops* (in the genus *Pseudostoma*), with type locality on the prairie road to Bent's Fort, near what is now the town of Las Animas, Bent County, Colorado. Later in the same year, Le Conte (1852) placed this taxon in the genus *Geomys*. Baird (1855) described *Geomys clarkii* as a species closely related to *castanops* from Presidio del Norte along the Rio Grande in Chihuahua. Coues (1875) later placed *G. clarkii* in synonymy with *G. castanops*.

Merriam (1895), in his monographic revision of the family Geomyidae, described the genera *Pappogeomys* and *Cratogeomys* with *G. merriami* as the type of *Cratogeomys*. He assigned specimens of *castanops* from the United States to this new genus as well. He also agreed with Coues (1875) as to the status of *clarkii* and described an additional subspecies, *Cratogeomys castanops goldmani*, from central México. Merriam (1895), however, examined only 30 specimens of the genus *Cratogeomys* from the United States.

Nearly 40 years elapsed before the next revision of the genus was undertaken (Nelson and Goldman, 1934). In that period of time, the systematic arrangement of Merriam (1895) had remained unchanged. Nelson and Goldman (1934), based on many additional specimens (they listed 68 from the United States as examined plus those of *C. c. castanops*,

which they did not list), resurrected *clarkii* as a subspecies of *castanops*, and described 13 additional races of that species. Four of these were from the United States, bringing the number of recognized races from north of the Rio Grande to five (they restricted the distribution of *C. c. clarkii* to south of the river).

No additional taxa of *C. castanops* from the United States were described until Russell (1968*b*) revised the genus *Pappogeomys*, within which he recognized *Cratogeomys* as a subgenus. Until that time, most authors, such as Simpson (1945) and Wood (1955), followed Merriam (1895) in recognizing *Cratogeomys* as a genus distinct from *Pappogeomys*.

Russell (1968*b*) examined a total of 448 specimens of *castanops* from the United States from which he described four additional subspecies. He placed *C. c. lacrimalis* Nelson and Goldman in synonymy under *C. c. perplanus* Nelson and Goldman, and allocated specimens from north of the Rio Grande in the Big Bend area of Texas to the subspecies *clarkii*. This increased the number of recognized races of *C. castanops* from the United States to nine.

Few studies of systematic importance dealing with *Cratogeomys* have appeared since Russell's (1968*b*) revision. Dowler and Genoways (1979) evaluated geographic variation of these gophers on the Llano Estacado of Texas and New Mexico, and found the subspecies *C. c. simulans* (Russell) from the eastern Llano to be indistinguishable from the earlier-named *C. c. perplanus* Nelson and Goldman from the western part of the Llano. In a study of the genic relationships of selected pocket gophers, Honeycutt and Williams (1982) found members of the subgenus *Cratogeomys* to be clearly distinct from those of the subgenus *Pappogeomys*, and suggested that the two subgenera were deserving of generic recognition. This systematic arrangement has been followed recently (Jones *et al.*, 1986; Lee and Baker, 1987).

In a study of the chromosomal relationships of taxa of *Cratogeomys*, Berry and Baker (1972) found two distinct chromosomal types of *castanops*—a northern group with 46 chromosomes and a southern group with 42. Lee and Baker (1987) suggested that the southern races of *castanops* should be recognized as specifically distinct from those to the north based upon analysis of differentially stained chromosomes. They noted that none of the southern types (with 42 chromosomes) occurs north of 25 degrees N latitude, thus none is found in the United States.

Two major distributional records have been reported since Russell's (1968*b*) study. Birney *et al.* (1971) reported *C. castanops* from Kansas. They allocated populations north of the Arkansas River in western Kansas to the nominate subspecies *castanops*, based upon their cranial measurements. Cleveland (1977) reported a population of *C. castanops* from the Texas side of the lower Rio Grande Valley near Brownsville. He did not assign these specimens to any subspecies, but noted that the nearest records were from Tamaulipas, México.

Fossil Record

In his treatise on the classification of the Geomyinae, Russell (1968*a*) indicated that *Pappogeomys* (including *Cratogeomys*) was not known from Pleistocene deposits older than Wisconsin times, but noted a pre-Pleistocene (Pliocene) occurrence in the Benson Beds of Arizona. Russell attributed this to a proposed southern distribution of the genus, probably on the central Mexican Plateau, an area where few early to middle Pleistocene deposits have been found. In outlining the intraspecific population structure of *Cratogeomys castanops*, Russell (1969) hypothesized the retreat of the genus from the southwestern United States during the Wisconsin pluvial cycle, with a subsequent postglacial reinvasion of the region. However, when depicting the proposed early Pleistocene geographic ranges of the geomyid genera (Russell, 1968*a*:fig. 2), he mapped the genus *Zygogeomys* as occupying the southwestern United States (most of the area currently occupied by *Cratogeomys*), with *Pappogeomys* (including *Cratogeomys*) restricted to the southern Mexican Plateau. Harris (1985) questioned Russell's (1969) hypothesized retreat of *Cratogeomys* from the southwestern United States during the Wisconsin by pointing out the occurrence of *Cratogeomys* at several stadial sites in the Guadalupe Mountains, indicating that populations occurred farther north during the Pleistocene than envisioned by Russell (1968*a*, 1969).

Other remains of *Cratogeomys* were reported by Rinker (1941) from Meade County, Kansas, from a Recent terrace, and by Gilmore (1947) as common in Quaternary cave deposits near Cuatro Ciénegas, Coahuila. Mooser and Dalquest (1975) reported *P.* cf. *castanops* remains from Pleistocene (probably Illinoian) deposits in Aguascalientes in central México. Harris (1987) reported *Pappogeomys* sp. from mid-Wisconsin deposits in Dry Cave, Eddy County, New Mexico. Graham (1987), in a compilation of Quaternary mammalian faunas of the southwestern plains, discussed *C. castanops* remains from the following Texas localities: Cueva Quebrada (late Pleistocene, > 14,000 years BP); Bonfire Shelter (approximately 10,200 BP); Baker Cave (Level IV, middle Holocene, 3000 to 6000 BP); Devil's Mouth (undifferentiated Holocene); Deadman's Shelter, Canyon City Club Cave (Level 1 to 5); Alibates 28, Roper, and Spring Canyon (all from late Holocene, 300 to 3000 BP).

Natural History

Little is known of the natural history of *Cratogeomys castanops*; most published information is anecdotal. Two recent papers (Davidow-Henry and Jones, 1988; Davidow-Henry *et al.*, 1989) summarized the biology of this species, and are the primary sources for the sections that follow.

Reproduction

Reproduction in Texas was summarized by Davidow-Henry and Jones (1988). Their data, and the data from Ikenberry (1964) and Smolen *et al.* (1980), indicate that pregnant females have been taken in every month, with an average of 2.08 fetuses per female. Davidow-Henry and Jones (1988) recorded lactating females from January, February, March, May, July, August, October, and December. Smolen *et al.* (1980) reported lactating females from April as well.

Davidow-Henry and Jones (1988) also reported the occurrence of juveniles in all months except September and December. They concluded that *C. castanops* is reproductively active throughout the year in Texas; they found no unusually marked peaks of reproductive activity. They agreed with Smolen *et al.* (1980) that at least some individuals bear multiple litters annually. Northwardly, in Colorado and Kansas, the breeding season of *C. castanops* probably is limited to the warmer months of the year, but only indirect evidence (Birney *et al.*, 1971) is available.

Molt

Davidow-Henry and Jones (1988) described the juvenile pelage of *C. castanops* as straw-colored or grayish yellow, contrasting markedly with the generally darker pelage of adults. They stated that postjuvenile molt evidently begins on the head and proceeds posteriorly to the level of the eyes and ears while proceeding ventrally over the cheeks and upper throat. They opined that the venter molted rapidly because they observed few animals in the process of ventral molt. From the head region, molt progressed caudally on the dorsum with the middorsal areas molting in advance of the flanks. The areas at the base of the tail and on the posterior flanks were the last regions to molt.

Birney *et al.* (1971) reported distinctive semiannual molts in adult *C. castanops* in Kansas. They found molt from winter to summer pelage early in spring and from summer to winter pelage in September and October. Ikenberry (1964), however, reported a single extended molting period, beginning in August and continuing through March in adult specimens from Lubbock County, Texas.

Habitat

Cratogeomys castanops frequently is found in deep, sandy soils that are relatively free of rocks (Schmidly, 1977; Davis, 1940). This pocket gopher generally inhabits valleys and avoids the hard soils of arid mesas and upper slopes (Bailey, 1905, 1932). Findley (1987) noted that in eastern New Mexico, *Cratogeomys* was excluded from deep, sandy soils and forced to survive in shallower, rocky soils in the presence of *Geomys*, a situation similar to that reported in Kansas by Birney *et al.* (1971). However, in the presence of *Thomomys*, *Cratogeomys* seems to exclude the former from the more pliable soils and force these smaller gophers into thin, rocky soils (Findley, 1987; Hollander *et al.*, 1987). The displacement of *Thomomys* by *Cratogeomys* has been documented in Limpia Canyon, Jeff Davis County, Texas (Reichman and Baker, 1972; Williams and Baker, 1976), and is known elsewhere where ranges of the two broadly overlap. Schmidly (1977) discussed shifts in the distributions of *Thomomys* and *Cratogeomys*, in an area of the Trans-Pecos, that corresponded to the available moisture, and opined that *Cratogeomys* seemed to be favored as conditions became more xeric. Moulton *et al.* (1979) reported an area of sympatry between *Cratogeomys* and *Thomomys* in southeastern Colorado. Moulton *et al.* (1983) discussed the ecological parameters that separated all three genera of gophers in southeastern Colorado. They found that where *Cratogeomys* and *Thomomys* occurred sympatrically, the latter had significantly shallower burrows. However, they concluded that the two genera were mutually exclusive competitors and the zone of sympatry probably represented an area where one species was displacing the other. Where *Cratogeomys* and *Geomys* came into contact, they found the latter to occupy disturbed soils, whereas the former was primarily restricted to native shortgrass rangeland.

From personal observations in the field, it is apparent that *Cratogeomys* occupies the most favorable soils that are available in an area. However, it is not restricted to such areas. For example, in the area of Independence Creek, in northern Terrell County, Texas, these gophers are common along the Pecos River and on a private golf course in the creek bottom. Both of these areas have relatively deep, pliable soils, but gophers also are common above the bottom land, in rocky, caliche type soils. A similar situation exists in western Upton and Crane counties and northeastern Pecos County, Texas, where gophers are abundant in the river bottom of the Pecos but also occur in upland areas characterized by soils that are extremely hard and rocky. It seems apparent from these observations, and those cited above, that *Cratogeomys castonops* is a generalist and has the ability to survive in many different types of habitat.

Materials and Methods

Three external measurements (total length, length of tail, and length of hind foot) were obtained from original specimen labels. However, variation among methods of individual preparators in measuring these external dimensions rendered them virtually useless for statistical analysis. They were excluded from further analyses in this study, but some external measurements (mm.) are listed in text.

Fifteen cranial and mandibular measurements, similar to those used in other studies of geomyids (Davis and Buechner, 1946; Villa-R. and Hall, 1947; Youngman, 1958; Russell, 1968*b*; Hendricksen, 1973; Smith *et al.*, 1983), were taken with Fowler digital calipers to the nearest 0.01 millimeters. Description of these measurements, depicted in Figure 1 (letters following measurement names correspond to the letters on the figures), follows.

Condylobasal length (A-A).—Shortest distance from posteriormost projection of occipital condyle to anteriormost projection of premaxilla.

Zygomatic breadth (B-B).—Greatest distance parallel to long axis of skull across zygomatic arches.

Mastoid breadth (C-C).—Greatest distance parallel to long axis of skull across mastoid process of squamosal bone.

Occipital depth (D-D).—Shortest distance perpendicular to long axis of skull from ventralmost portions of auditory bullae to temporal ridge of squamosals.

Breadth of rostrum (E-E).—Greatest width across rostrum anterior to zygomatic arches.

Length of rostrum (F-F).—Distance from anteriormost projection of nasal to lateral junction of lacrimal and maxilla.

Length of nasals (G-G).—Greatest distance from anteriormost to posteriormost point of nasals.

Interorbital constriction (H-H).—Least width across frontals.

Palatofrontal depth (I-I).—Shortest distance perpendicular to long axis of skull between frontals and palatine bones between molars.

Alveolar length of maxillary toothrow (J-J).—Distance from anterior lip of alveolus of P4 to posterior lip of alveolus of M3.

Length of palate (K-K).—Shortest distance from anteriormost point on posterior border of palate to posterior lip of alveolus of incisors.

Width of upper incisor (L-L).—Greatest width of incisor immediately distal to alveolus.

Alveolar length of mandibular toothrow (M-M).—Distance from anterior lip of alveolus of p4 to posterior lip of alveolus of m3.

Depth of ramus (N-N).—Shortest perpendicular distance from angle of mandible to dorsalmost point of coronoid process.

Width of lower incisor (O-O).—Greatest width of incisor immediately distal to alveolus.

Multivariate tests were employed to detect group differences before any univariate tests were used. Willig *et al.* (1986) and Willig and Owen (1987) have demonstrated that the results of multiple univariate tests (for example, 15 ANOVAs on 15 characters) do not emulate the results of a multivariate test (MANOVA on 15 characters); and when analyzing morphological variation in natural populations, it is a multivariate question that is asked. However, for an alternative view, see Corruccini (1987).

All statistical tests used (both multivariate and univariate) are from programs available in the SPSS^x statistical package (SPSS Inc., 1986). Specific tests utilized in particular phases of the analyses are discussed in

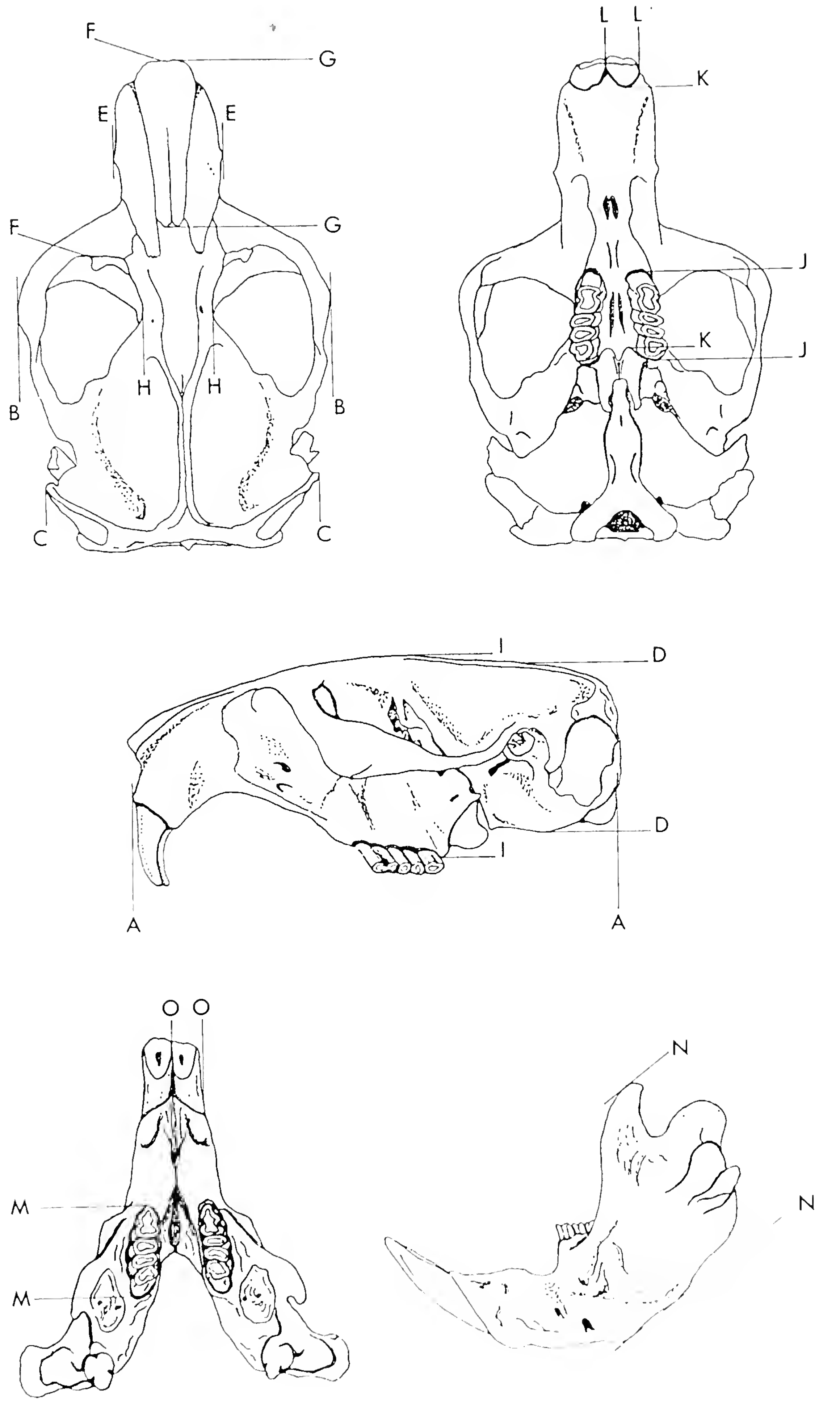

FIG. 1.—Dorsal, ventral, and lateral views of the skull and dorsal and lateral views of the mandible of an adult female *Cratogeomys castanops* (TTU 1524) from 8 mi. N Lubbock, Lubbock Co., Texas. Letters correspond to measurements described in text.

more detail in the following sections on nongeographic and geographic variation.

The accounts of the subspecies begin with an abbreviated synonymy that includes: 1) the original description with citation and type locality; 2) citation to the first use of the current name combination (if any); and 3) any junior synonyms in chronological order with their respective citations and type localities. The synonymy is followed by a short section describing the geographic distribution of the subspecies. Next is a morphological description of the taxon followed by a section on comparisons with adjacent taxa. This is followed by a remarks section and a list of specimens examined.

Localities from which specimens were examined are mapped and listed in the specimens examined section following each account. Not all localities are plotted as undue crowding of symbols would have resulted and, for the same reason, some symbols are slightly offset on the figures. Those localities not mapped are in italic type in the lists of specimens examined. Localities for a given taxon are listed alphabetically by state and by county within a state. Within a county, localities are listed from north to south and west to east.

In the course of plotting specimen localities, some were found to have specific localities that did not match the county designation on the label. In such cases, it was assumed that the specific locality was the correct site of capture. These specimens are listed under what is believed to be the correct county, with a note as to the county that was recorded on the original specimen label.

I am indebted to the individuals from the following institutions, with accompanying acronyms corresponding to those used in the lists of specimens examined in the following accounts, for loan of material or for allowing me access to collections in their care. AMNH—American Museum of Natural History, Sydney Anderson and Guy G. Musser. ASU—Angelo State University, Mark D. Engstrom. CCSU—Corpus Christi State University, Brian R. Chapman. ENMU—Eastern New Mexico University, Antonio L. Gennaro. KU—Museum of Natural History, University of Kansas, Robert M. Timm. MHP—Museum of the High Plains, Ft. Hays State University, Jerry R. Choate. MSB—Museum of Southwest Biology, University of New Mexico, Terry L. Yates. MVZ—Museum of Vertebrate Zoology, University of California Berkley, James L. Patton. MWSU—Midwestern State University, Walter W. Dalquest and Fredrick B. Stangl, Jr. NMSU—New Mexico State University, Charles S. Thaeler, Jr. OMNH—Oklahoma Museum of Natural History, University of Oklahoma, Michael A. Mares. OSU—Oklahoma State University, David Edds. SRSU—Sul Ross State University, James F. Scudday. TAI—Texas A&I University, Allan H. Chaney. TCWC—Texas Cooperative Wildlife Collection, Texas A&M University, David J. Schmidly. TNHC—Texas Natural History Collection, University of Texas Austin, Robert F. Martin.

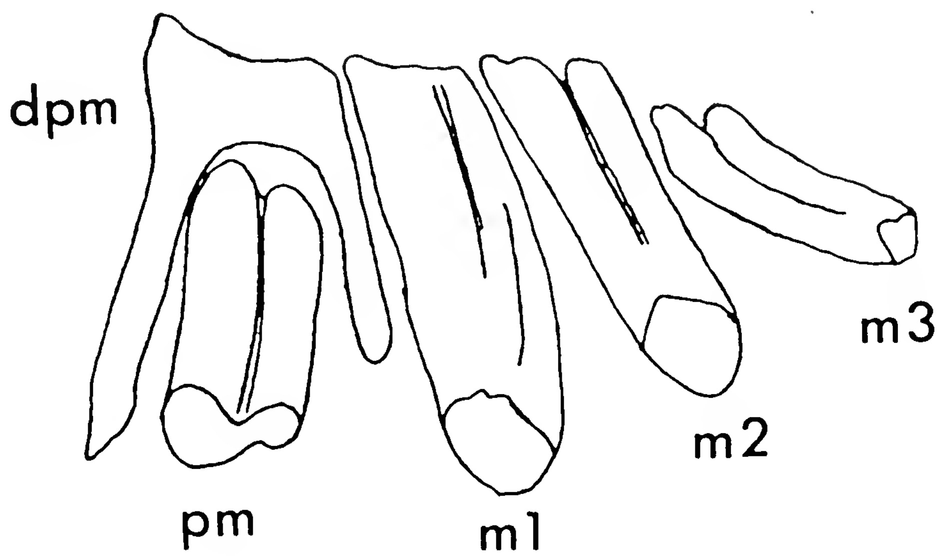

FIG. 2.—Lateral view of the lower toothrow of a typical juvenile geomyid showing the relationship of the deciduous premolar and permanent premolar (after Merriam, 1895).

TTU—Texas Tech University, Robert J. Baker (specimens for which no acronym is listed are in this collection). TWC—Texas Wesleyan College, Arthur G. Clevland. UCM—University of Colorado Museum, David M. Armstrong. UIMNH—University of Illinois Museum of Natural History, M. Raymond Lee. USNM—National Museum of Natural History, Don E. Wilson and Robert Fisher. UTEP—University of Texas El Paso, Arthur H. Harris. WTSU—West Texas State University, Flavius C. Killebrew.

Nongeographic Variation

Specimens of *Cratogeomys castanops* were allocated to one of five age classes (one through five) based on criteria modified from Merriam (1895) and Russell (1968 *b*). To document the amount of morphological variation that is attributable to secondary sexual, age, or individual variation, a sample of 184 individuals from Lubbock County, Texas (the largest single sample available), was analyzed. Within this sample, both sexes and all the age classes (except age class one and females of age class five) were well represented (see Table 1 for sample sizes within each class).

Juvenile (age class 1).—Both upper and lower deciduous premolars present (see Fig. 2). Only one specimen from this age class was examined. Merriam (1895) reported that juveniles were extremely rare (he examined only four in the entire family, none of them *Cratogeomys*). Russell (1968 *b*) did not mention any juveniles and Dowler and Genoways (1979) stated that they did not examine any among 473 individuals from the Llano Estacado of Texas and New Mexico.

Young (age class 2).—Both upper and lower permanent premolars present. Exoccipital-supraoccipital suture unfused in both sexes. Few sutures of the skull are fused and the bones are quite porous. Skulls appear rounded when viewed laterally. Young individuals evidenced juvenile pelage as described by Davidow-Henry and Jones (1988).

Subadult (age class 3).—Supraoccipital-exoccipital suture fused but the basioccipital-basisphenoid suture unfused in both sexes. Temporal ridges present but not in contact with each other in either sex, but more prominent in males. Many subadults (approximately 50 percent) exhibited adult pelage.

Adult (age class 4).—Females: temporal ridges in contact or basioccipital-basisphenoid suture fused and obliterated. Only a few individuals that had the temporal ridges in contact did not have a fused basioccipital-basisphenoid suture, but an occasional individual with the suture fused did not have temporal ridges in contact. Males: temporal ridges in contact but basioccipital-basisphenoid suture unfused.

Old adult (age class 5).—Occasional females with a pronounced sagittal crest and overall angular skull. In males, basioccipital-basisphenoid suture fused and obliterated, accompanied by large sagittal crest and much angularity to the skull. Many more old adult males were examined than females.

Table 1 provides standard descriptive statistics (for combination of age class and sex) for the Lubbock County sample.

A two-way multivariate analysis of variance (MANOVA), with sex and age as the main factors, was performed using program MANOVA from SPSS^x (SPSS, Inc., 1986). Highly significant results ($P < 0.001$) were obtained for each main effect, which indicated significant differences between sexes and between at least some of the age classes. The absence of a significant sex by age interaction indicated that males differed from

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Breadth of Rostrum			
		Males			
2	24	9.663	0.541	0.110	8.82-10.79
3	17	11.004	0.499	0.121	10.28-12.23
4	33	12.472	1.295	0.225	10.31-14.72
5	8	13.839	0.833	0.295	12.60-15.31
		Females			
2	22	9.527	0.835	0.178	7.67-10.84
3	30	10.579	0.625	0.114	9.13-11.94
4	49	11.322	0.491	0.070	10.35-12.64
		Length of Rostrum			
		Males			
2	24	19.018	1.353	0.276	16.76-21.87
3	17	22.721	0.899	0.218	21.43-24.68
4	32	24.885	2.056	0.363	21.11-27.63
5	8	27.543	1.009	0.357	25.95-28.90
		Females			
2	21	18.601	1.708	0.373	14.99-20.90
3	29	21.465	1.083	0.201	18.88-23.85
4	46	22.921	1.033	0.152	21.15-24.86
		Length of Nasals			
		Males			
2	24	15.620	1.262	0.258	13.07-18.17
3	17	18.975	1.005	0.244	17.02-20.51
4	32	21.041	1.890	0.334	17.18-24.04
5	8	23.595	1.037	0.367	22.20-25.23
		Females			
2	21	15.313	1.586	0.346	12.08-17.06
3	29	18.105	1.131	0.210	15.08-20.26
4	46	19.390	0.864	0.127	17.84-21.09
		Interorbital Constriction			
		Males			
2	24	6.752	0.282	0.058	6.23-7.26
3	17	6.788	0.554	0.134	5.82-7.85
4	33	6.899	0.496	0.086	6.11-7.95
5	8	6.515	0.340	0.120	6.07-7.18
		Females			
2	22	6.592	0.339	0.072	5.69-7.30
3	30	6.835	0.390	0.071	6.24-7.85
4	49	6.825	0.376	0.054	6.15-7.66

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Palatofrontal Depth			
		Males			
2	24	17.728	0.850	0.174	16.19-19.16
3	17	19.772	0.603	0.146	18.96-20.98
4	33	21.502	1.571	0.273	18.09-24.03
5	8	23.649	0.882	0.312	22.42-24.97
		Females			
2	22	17.406	1.226	0.262	14.84-18.87
3	30	18.986	0.703	0.128	17.84-20.65
4	49	20.114	0.815	0.117	18.25-21.76
		Length of Maxillary Toothrow			
		Males			
2	24	9.025	0.486	0.099	8.27-10.10
3	17	9.805	0.452	0.110	9.13-10.66
4	33	10.322	0.468	0.081	9.69-11.75
5	8	10.839	0.395	0.140	10.30-11.39
		Females			
2	22	8.953	0.568	0.121	7.70-10.05
3	30	9.682	0.396	0.072	9.00-10.53
4	49	9.992	0.416	0.059	9.02-11.39
		Length of Palate			
		Males			
2	24	23.793	1.649	0.337	20.79-26.73
3	17	28.299	1.030	0.250	27.10-30.69
4	32	31.278	2.200	0.389	27.40-35.12
5	8	34.028	1.233	0.436	32.47-36.22
		Females			
2	22	23.442	2.314	0.493	18.52-26.98
3	30	27.072	1.281	0.234	24.07-29.32
4	49	28.875	1.182	0.169	26.62-31.72
		Width of Upper Incisor			
		Males			
2	24	2.454	0.215	0.044	2.08-2.96
3	17	2.991	0.108	0.026	2.79-3.17
4	33	3.393	0.289	0.050	2.89-3.98
5	8	3.678	0.198	0.070	3.37-3.93
		Females			
2	22	2.468	0.285	0.061	1.84-3.03
3	30	2.878	0.159	0.029	2.50-3.21
4	48	3.065	0.096	0.014	2.88-3.27

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Length of Mandibular Toothrow			
		Males			
2	24	8.434	0.335	0.068	7.88-9.09
3	17	8.991	0.214	0.052	8.52-9.34
4	33	9.383	0.372	0.065	8.68-10.21
5	8	9.898	0.380	0.134	9.33-10.51
		Females			
2	22	8.387	0.492	0.105	7.40-9.68
3	30	8.928	0.373	0.068	8.22-9.57
4	49	9.207	0.304	0.044	8.63-10.34
		Depth of Ramus			
		Males			
2	24	15.768	0.699	0.143	14.68-17.33
3	17	17.903	0.618	0.150	17.03-18.97
4	33	18.858	1.134	0.198	17.19-21.29
5	8	19.949	0.526	0.186	19.11-20.84
		Females			
2	22	15.621	1.072	0.229	13.35-17.18
3	30	17.093	0.835	0.152	15.63-19.36
4	49	17.698	0.694	0.099	16.30-19.13
		Width of Lower Incisor			
		Males			
2	24	2.315	0.196	0.040	1.96-2.77
3	17	2.882	0.118	0.029	2.70-3.11
4	33	3.273	0.322	0.056	2.72-3.95
5	8	3.528	0.173	0.061	3.30-3.71
		Females			
2	22	2.323	0.310	0.066	1.57-2.87
3	30	2.755	0.168	0.031	2.42-3.08
4	49	2.924	0.120	0.017	2.71-3.21

females in a consistent fashion regardless of age. Because of the highly significant difference between sexes and the nonsignificant interaction, males and females were separated for all subsequent analyses.

To ascertain which age classes were significantly different within each sex, one-way analysis of variance (ANOVA) was performed on each variable with age as the main factor. The results of these analyses are presented in Table 2. If significant results ($P < 0.05$) were obtained due to the effects of age, three different *a posteriori* multiple range tests (Student-Newman-Keuls, Scheffe's, and Duncan's—Sokal and Rohlf, 1981) were employed to

TABLE 2.—*Results of the one-way ANOVAs with age as the main factor for each sex for the sample of* Cratogeomys castanops *from Lubbock County, Texas. Given are source of variation (between groups, within groups, and total variation), degrees of freedom (DF), sum of squares (SS), mean square (MS), F ratio (F), and significance level (P).*

Source	DF	SS	MS	F	P
		Condylobasal Length			
		Males			
Between	3	2410.209	803.403	99.938	< 0.001
Within	78	627.042	8.039		
Total	81	3037.251			
		Females			
Between	2	886.013	443.007	89.011	< 0.001
Within	94	467.839	4.977		
Total	96	1353.852			
		Zygomatic Breadth			
		Males			
Between	3	1790.948	596.983	90.354	< 0.001
Within	76	502.145	6.607		
Total	79	2293.094			
		Females			
Between	2	549.752	274.876	78.702	< 0.001
Within	97	338.783	3.493		
Total	99	888.536			
		Mastiod Breadth			
		Males			
Between	3	638.770	212.924	72.080	< 0.001
Within	76	224.502	2.954		
Total	79	863.273			
		Females			
Between	2	210.989	105.494	61.460	< 0.001
Within	94	161.349	1.717		
Total	96	372.338			
		Occipital Depth			
		Males			
Between	3	183.061	61.020	67.308	< 0.001
Within	78	70.713	0.907		
Total	81	253.774			
		Females			
Between	2	69.677	34.838	71.302	< 0.001
Within	96	46.906	0.489		
Total	98	116.582			

TABLE 2.—*Continued.*

Source	DF	SS	MS	F	P
		Palatofrontal Depth			
		Males			
Between	3	300.589	100.196	73.146	< 0.001
Within	78	106.845	1.370		
Total	81	407.434			
		Females			
Between	2	113.112	56.556	71.225	< 0.001
Within	98	77.817	0.794		
Total	100	190.929			
		Length of Maxillary Toothrow			
		Males			
Between	3	31.441	10.480	48.714	< 0.001
Within	78	16.781	0.215		
Total	81	48.221			
		Females			
Between	2	16.383	8.191	40.919	< 0.001
Within	98	19.618	0.200		
Total	100	36.001			
		Length of Palate			
		Males			
Between	3	1020.393	340.131	109.009	00.001
Within	77	240.257	3.120		
Total	80	1260.650			
		Females			
Between	2	448.412	224.206	96.762	< 0.001
Within	98	227.074	2.317		
Total	100	675.486			
		Width of Upper Incisor			
		Males			
Between	3	15.594	5.198	96.675	< 0.001
Within	78	4.194	0.054		
Total	81	19.788			
		Females			
Between	2	5.373	2.687	90.633	< 0.001
Within	97	2.876	0.030		
Total	99	8.249			

TABLE 2.—*Continued.*

Source	DF	SS	MS	F	P
		Breadth of Rostrum			
		Males			
Between	3	160.101	53.367	60.137	< 0.001
Within	78	69.219	0.887		
Total	81	229.320			
		Females			
Between	2	49.659	24.829	64.828	< 0.001
Within	98	37.534	0.383		
Total	100	87.193			
		Length of Rostrum			
		Males			
Between	3	660.507	220.169	87.782	< 0.001
Within	77	193.127	2.508		
Total	80	853.634			
		Females			
Between	2	269.361	134.681	89.992	< 0.001
Within	93	139.183	1.497		
Total	95	408.544			
		Length of Nasals			
		Males			
Between	3	571.126	190.375	85.710	< 0.001
Within	77	171.029	2.221		
Total	80	742.154			
		Females			
Between	2	239.671	119.836	93.078	< 0.001
Within	93	119.735	1.288		
Total	95	359.407			
		Interorbital Constriction			
		Males			
Between	3	1.031	0.344	1.739	0.166
Within	78	15.412	0.198		
Total	81	16.442			
		Females			
Between	2	0.963	0.482	3.467	0.035
Within	98	13.611	0.139		
Total	100	14.574			

TABLE 2.—*Continued.*

Source	DF	SS	MS	F	P
		Length of Mandibular Toothrow			
		Males			
Between	3	18.527	6.176	55.081	< 0.001
Within	78	8.745	0.112		
Total	81	27.272			
		Females			
Between	2	10.225	5.112	36.963	< 0.001
Within	98	13.554	0.138		
Total	100	23.779			
		Depth of Ramus			
		Males			
Between	3	172.838	57.613	74.329	< 0.001
Within	78	60.458	0.775		
Total	81	233.296			
		Females			
Between	2	65.547	32.773	47.613	< 0.001
Within	98	67.456	0.688		
Total	100	133.003			
		Width of Lower Incisor			
		Males			
Between	3	15.871	5.290	89.163	< 0.001
Within	78	4.628	0.059		
Total	81	20.499			
		Females			
Between	2	5.481	2.741	76.065	< 0.001
Within	98	3.531	0.036		
Total	100	9.012			

identify nonsignificant subsets of the age classes, and the results were compared for congruence. The experiment-wise error rate for all tests was 0.05. Both Student-Newman-Keuls and Scheffe's procedures are relatively conservative tests, whereas Duncan's test is more sensitive (Sokal and Rohlf, 1981). Scheffe's procedure is mathematically equivalent to sums-of-squares simultaneous testing procedure (SS-STP) that has been used in previous systematic analyses (Genoways, 1973).

In males, all of the characters save interorbital constriction were highly significant for variation due to age. For all significant variables, the *a posteriori* tests identified four significantly different subsets that corresponded to the four age classes (two through five). This indicates that these four age classes are each morphometrically distinct and should not be pooled in systematic analysis of morphometric variation.

For females, all of the characters were significant for variation due to age. Interorbital constriction was the only character that was not highly significant ($P > 0.001$). Moreover, only two significantly different subsets were formed in the *a posteriori* tests for this variable. The Student-Newman-Keuls and Duncan's procedures each formed subsets of age class two and another of age classes four and three, whereas the Scheffe's procedure produced subsets of age classes two and four and another of age classes four and three. For all other variables, three significantly different subsets that corresponded to the three age classes (two through four) were formed with the *a posteriori* tests.

In previous studies (Russell, 1968*b*; Dowler and Genoways, 1979), age classes four and five were combined in the comparisons of geographic groups. Based upon the results of this analysis, which is based on the largest single series of specimens available for study to date, the pooling of these two age classes could bias the results of the overall analysis of sexual or geographic variation.

Geographic Variation

For the analysis of geographic variation, localities were pooled to form groups of adequate sample size for statistical analyses, following the methodologies outlined by Genoways (1973). Care was taken not to cross potential biogeographic boundaries nor current taxonomic boundaries when forming groups. Specimens from peripheral or intermediate localities were not allocated to *a priori* groups, but subsequently were treated as unknowns. A general description of the resultant 22 groups (Fig. 3) follows, using abbreviated localities (see specimens examined in subspecies accounts beyond for complete localities).

Group 1.—Finney, Ford, Gray, Hodgeman, and Lane counties, Kansas.
Group 2.—Bacca, Bent, Huerfano, Las Animas, Otero, Prowers, and Pueblo counties, Colorado.
Group 3.—Union County, New Mexico.
Group 4.—Northwestern Cimarron County, Oklahoma, vicinity of Kenton.
Group 5.—Ochiltree, Hansford, Sherman, and Moore counties, Texas, and Texas and Beaver counties, Oklahoma.
Group 6.—Armstrong, Randall, and Potter counties, Texas.
Group 7.—Deaf Smith and Parmer counties, Texas.
Group 8.—Lamb, Hale, Floyd, Hockley, Lubbock, Terry, Lynn, Gaines, and Dawson counties, Texas.
Group 9.—De Baca, Roosevelt, Chaves, Lea, and Eddy counties, New Mexico, and Loving, Winkler, Ward, and northern Reeves counties, Texas.
Group 10.—Southern Howard, Glasscock, Sterling, Reagan, and Irion counties, Texas.
Group 11.—Northern Terrell County, Texas, vicinity of Independence Creek.
Group 12.—Southern Terrell County, Texas, vicinities of Sanderson and Dryden.
Group 13.—Southeastern Culberson (vicinity of Kent), southwestern Reeves (vicinity of Balmorea), northern Brewster (vicinity of Alpine), and Jeff Davis counties, Texas.
Group 14.—Southern Brewster County, vicinity of Big Bend National Park, Texas.
Group 15.—Southern Presidio County, vicinity of Presidio, Texas.
Group 16.—Southern Hudspeth County (vicinity of Sierra Blanca) and southwestern Culberson County (vicinity of Van Horn), Texas.
Group 17.—Northwestern Hudspeth (vicinity of Hueco Tanks) and El Paso counties, Texas.
Group 18.—Otero County, vicinity of White Sands National Monument, New Mexico.
Group 19.—Sierra County, vicinity of Rhodes Pass, New Mexico.
Group 20.—Lincoln County, vicinity of Carrizozo, New Mexico.
Group 21.—Maverick County, vicinity of Eagle Pass, Texas.
Group 22.—Cameron County, vicinity of Brownsville, Texas.

The presence of significant geographic variation within sexes but among groups was tested by a MANOVA. For both males and females, highly significant ($P < 0.001$) differences were obtained, indicating some morphometric differentiation between at least some *a priori* groups. The 15 cranial characters were then subjected to one-way ANOVAs with the *a priori* groups as the main effects for each sex. If significance was detected, indicating differences between *a priori* groups, the characters were then subjected to Student-Newman-Keuls, Scheffe's, and Duncan's multiple range tests. Although each of the 15 cranial characters were significant, for both males and females, the results of the multiple range tests indicated that many of

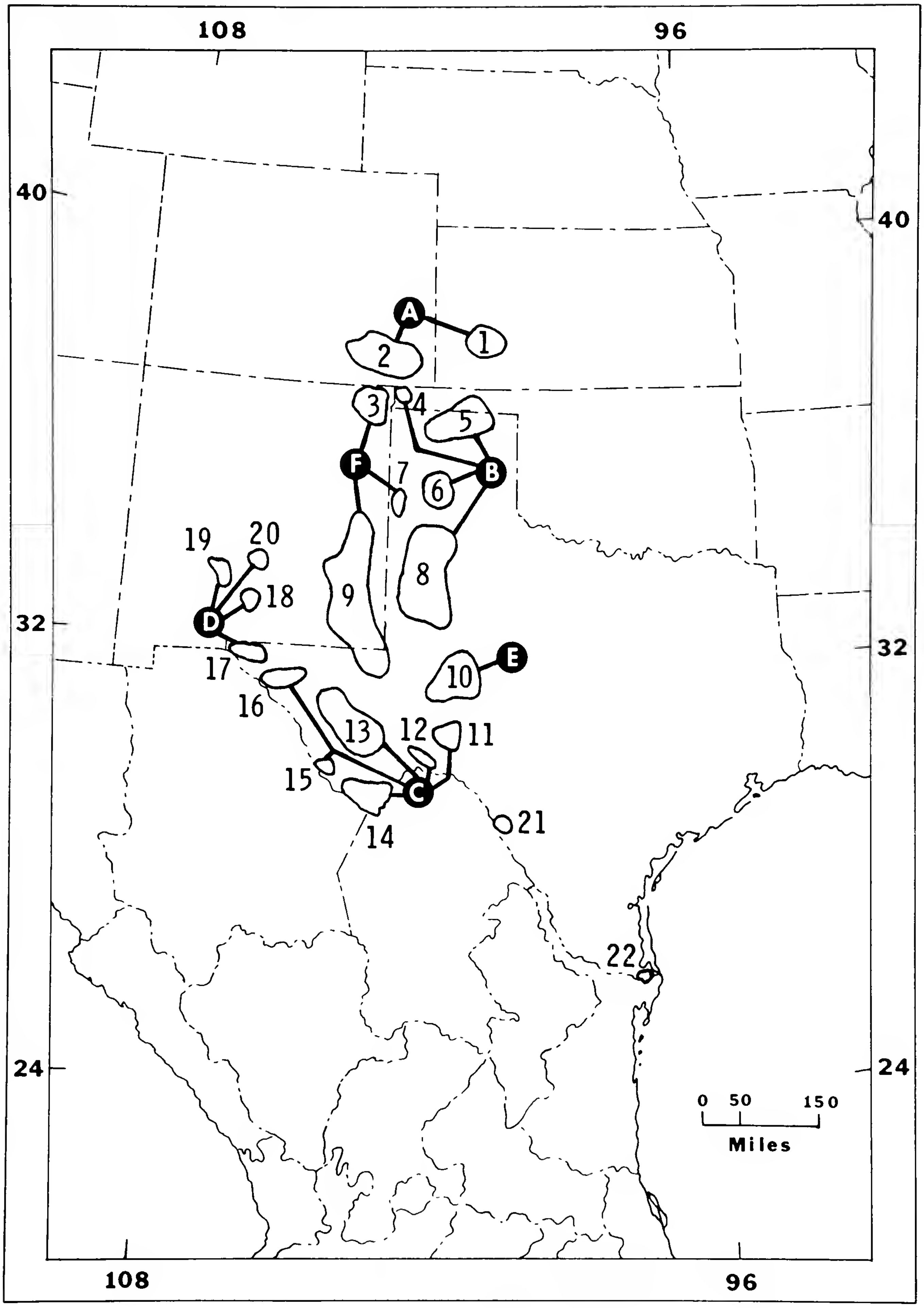

FIG. 3.—Map showing the 22 *a priori* groups (1-22) of *C. castanops* recognized from the United States and the six clusters (A-F) formed in the cluster analysis.

the *a priori* groupings were indistinct. Similar methodologies have been utilized with similar results in other morphometric analyses of mammalian species (Genoways, 1973; Willig, 1985; Riddle and Choate, 1986).

The following heuristic methodologies and *a priori* rational were utilized to determine whether any of the *a priori* groups (described above) could be pooled in subsequent analyses. Groups 21 and 22 (which are geographically isolated from the main distribution of the species in the United States) had such small sample sizes that their inclusion in multivariate analyses was not appropriate. Each of the remaining 20 groups was treated as an operational taxonomic unit (OTU—Sneath and Sokal, 1973), and, as in previous studies (Genoways, 1973; Riddle and Choate, 1986), the characters for each OTU were the means of the characters for that group. However, only the females of each group were utilized in this procedure because most taxonomic work on this species, and geomyids in general, historically, has been based on females (Russell, 1968*b* ; Hendricksen, 1973), which are much less variable within geographic groups than males. A cluster analysis (CA) based on a distance matrix was performed to ascertain which OTUs clustered together and thus resembled each other most closely morphologically. A principle component (PC) analysis also was performed and the first three components extracted. The PC scores on the first three components then were plotted to ascertain if there were phenetic relationships among OTUs that were comparable to the clusters found in the cluster analysis. If there was congruence between the results of the cluster analysis and the PCA, and if the OTUs that clustered together were geographically adjacent, then these were pooled in further analyses.

The cluster analysis (program CLUSTER, SPSS Inc., 1986) performed on these data used the squared Euclidian distance matrix. An unweighted pair-group method using arithmetic averages (UPGMA) was the chosen algorithm of agglomeration. The results of the cluster analysis are illustrated in Figure 4. Based on these results, five geographic clusters were formed as follows: A—groups 1 and 2; B—groups 4, 5, 6, and 8; C—groups 11, 12, 13, 14, 15, and 16; D—groups 17, 18, 19, and 20; E—groups 3, 7, 9, and 10. Only one of the clusters (cluster E) contained groups that were not geographically adjacent. Group 10 was geographically separated from the others in this cluster by group 8 of cluster B and by unsuitable habitat. Due to this geographic separation, group 10 was treated as a distinct cluster (cluster E) and the other groups (3, 7, and 9) as cluster F (Fig. 3). The PCA (program FACTOR) was performed on the OTUs and the first three components were extracted. The PC scores on the first three axes for each OTU were plotted and the results demonstrated in Figure 5. Examination of Figure 5 illustrates that the phenetic relationships among OTUs indicated by the results of the PCA correspond well with the results of the CA with the exception of cluster F, which appears to be a heterogeneous cluster.

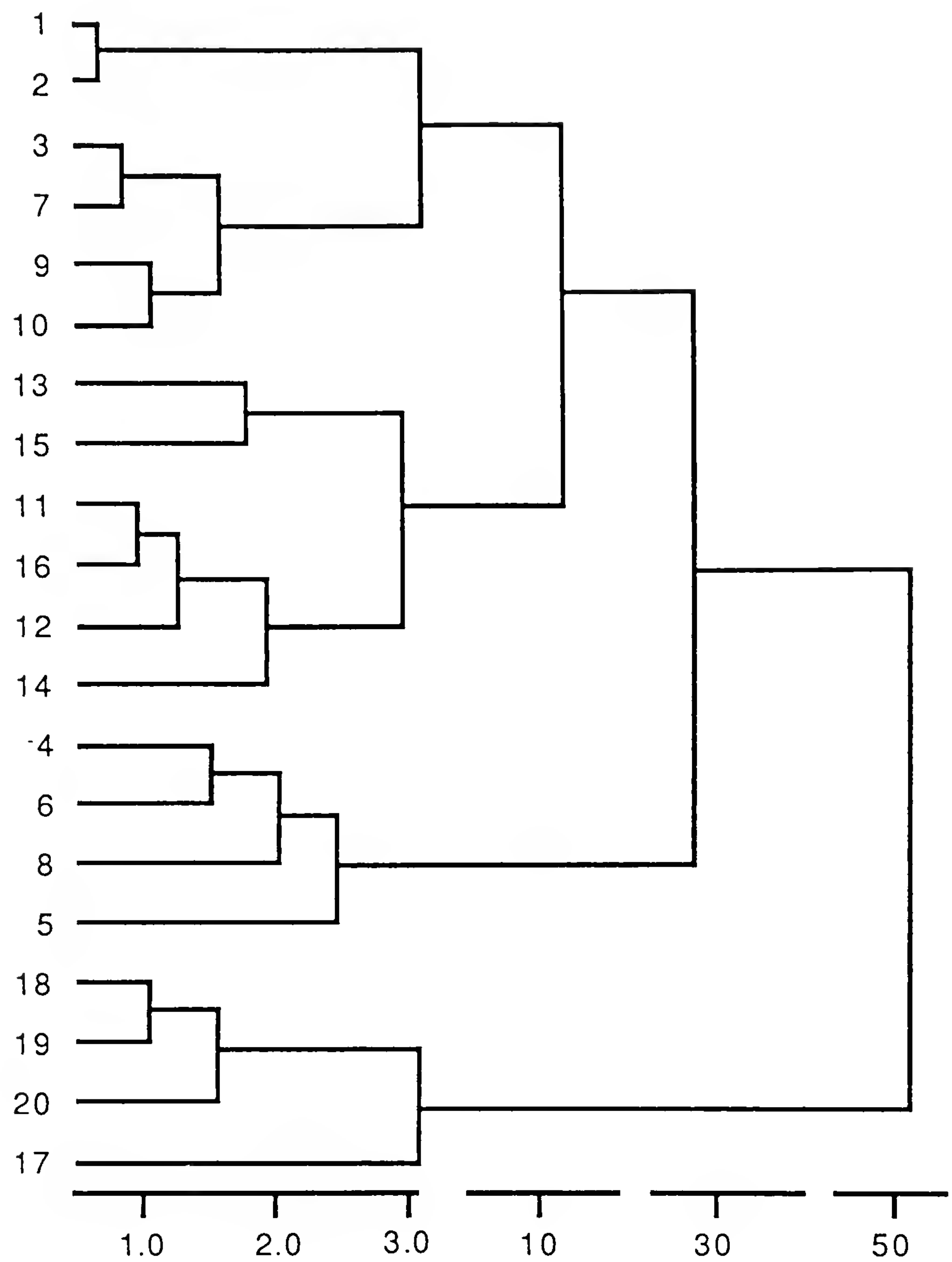

FIG. 4.—Phenogram depicting the results of the cluster analysis (see Fig. 3 for geographic location of samples). Note that the distance scale below the phenogram is nonlinear.

A two-way MANOVA was performed on the raw data with sex and clusters as the main effects. Highly significant ($P < 0.001$) differences among clusters within sexes and a nonsignificant interaction were obtained. These results indicated the presence of morphological differences between clusters that were consistent within the sexes. A discriminant function analysis (DFA—program DISCRIMINANT) then was employed to ascertain how well the individuals within these geographic clusters could be distinguished. In all of the clusters save F, individuals were correctly classified more than 60 percent of the time, whereas individuals within cluster F were correctly classified less than 30 percent of the time. The misclassified individuals of cluster F were not, however, assigned membership to any one of the other clusters more frequently than to any other.

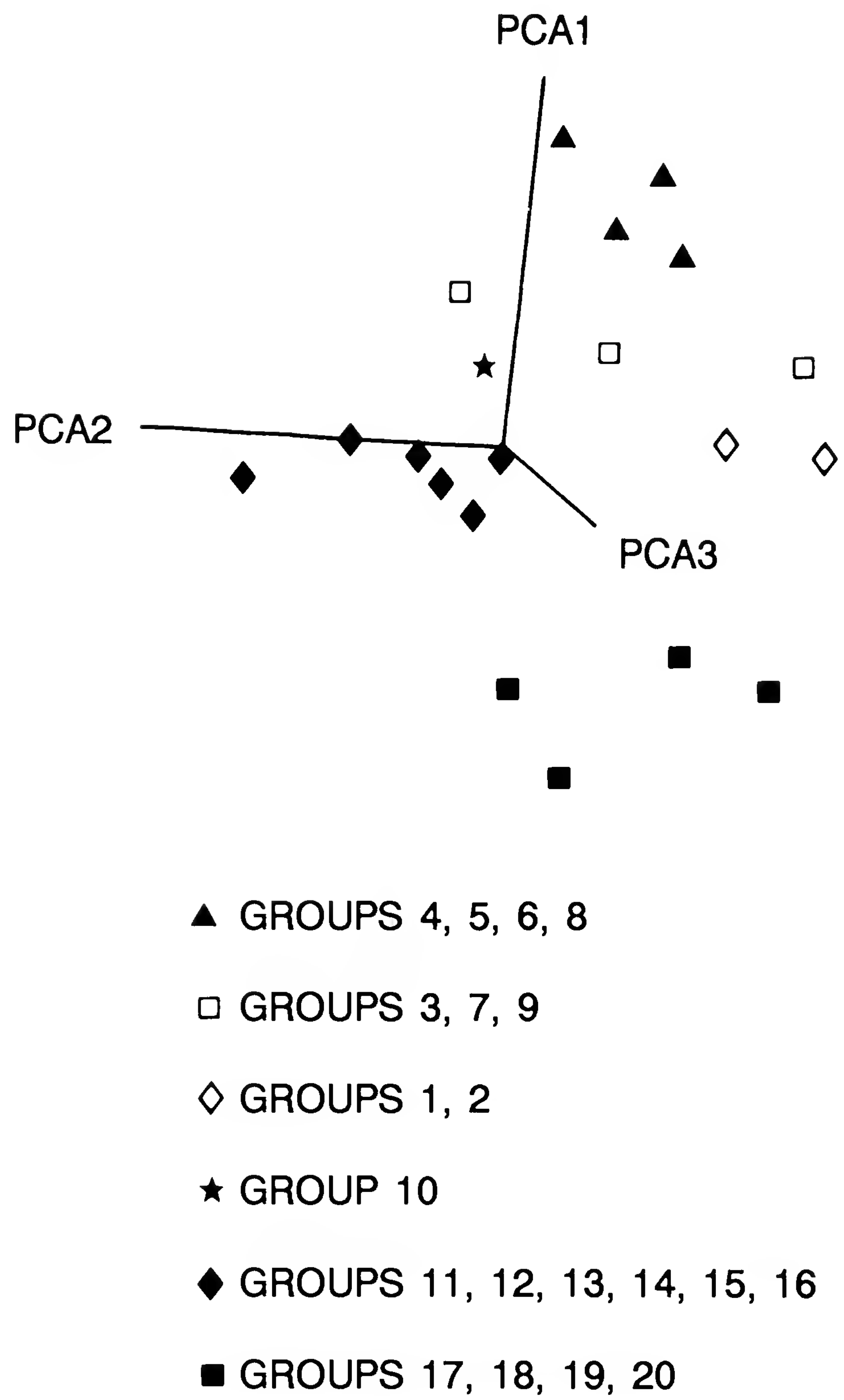

FIG. 5.—Three-dimensional plot of the first three principle components of the 20 groups used in the cluster analysis (see Fig. 3 for geographic location of samples).

Thus, no strong morphological affinity with any of the other clusters was indicated. These results, along with the results of the PCA (see Fig. 5), indicate that cluster F is a heterogeneous unit. All individuals from this cluster were treated as unknowns in subsequent analyses, leaving five clusters (A-E) to be tested (Fig. 3).

Another DFA was performed on individuals using these five clusters (A-E). The result was an overall correct classification rate of 80.7 percent for females (upon which the clusters were based) and 77.55 percent for males.

Table 3.—*Results of the discriminant function classification using the five clusters formed by cluster analyses. The columns are the clusters into which individuals were classified and the rows are the clusters to which the individuals belong.*

Groups	A	B	C	D	E
		Males			
A	36	4	1	0	0
B	10	58	1	0	2
C	1	3	42	4	3
D	0	1	8	14	0
E	0	4	1	0	6
		Females			
A	33	6	3	0	3
B	5	110	5	0	4
C	0	4	91	6	6
D	0	0	9	20	0
E	1	5	9	0	26

Table 3 shows the number of individuals from each cluster that were misclassified and into which cluster they were assigned membership. The individuals of cluster F (groups 3, 7, and 9; see Fig. 3), which were treated as unknowns in this analysis, were assigned membership to one of the five clusters (A-E) with the following results: all individuals but one of group 3 were assigned to cluster B; all individuals of group 7 were assigned to cluster B; individuals of group 9 were assigned with approximately equal frequency to clusters A, B, C, and E, indicating no apparent morphological affinities with any one cluster.

One-way ANOVAs (program ONEWAY) were performed on each of the 15 cranial characters for each sex separately with the geographic clusters as the main effect. For all characters that were significant for geographic variation, the three previously mentioned multiple range tests were employed to identify maximally nonsignificant subsets of clusters. The results of these tests are shown in Table 4.

Fourteen of the 15 characters were highly significant ($P < 0.001$) for geographic variation in both males and females. Interorbital constriction was significant ($P < 0.006$) in females but nonsignificant ($P > 0.05$) in males. For four of the characters (mastoid breadth, length of rostrum, width of upper incisor, and depth of ramus), five significantly different subsets that corresponded to the five groups (A-E) were identified among females. The remaining characters, with the exception of interorbital constriction, formed four significantly different subsets in females but the groups that

TABLE 4.—*Results of the one-way ANOVAs on each of the 15 cranial characters with the five clusters as the main effect for each sex. Also the results of Student-Newman-Keuls multiple range test (MRT) (Scheffes and Duncans gave similar results). Asterisks (*) in a column (MRT) indicate nonsignificant subsets of the clusters.*

Group	MRT					Mean	Range	P
						Condylobasal Length		
						Males		
D	*					49.66	45.88-53.65	< 0.001
C		*				52.61	46.76-57.13	
A		*	*			53.76	45.64-59.97	
E			*	*		55.10	47.87-57.90	
B				*		55.82	49.03-61.14	
						Females		
D	*					45.23	42.88-47.67	< 0.001
C		*				47.85	43.97-54.69	
A			*			48.78	46.65-52.36	
E			*			49.26	45.69-52.95	
B				*		51.25	48.28-55.22	
						Zygomatic Breadth		
						Males		
D	*					32.64	27.97-35.54	< 0.001
C		*				34.84	29.98-40.45	
A		*				35.87	31.57-41.10	
B			*			37.61	30.85-43.00	
E			*			37.71	32.32-40.35	
						Females		
D	*					28.14	26.48-29.76	< 0.001
C		*				30.56	27.26-38.82	
A		*				30.87	28.75-33.54	
E			*			31.47	28.43-33.86	
B				*		33.16	30.10-36.16	
						Mastoid Breadth		
						Males		
D	*					29.09	26.64-31.53	< 0.001
A		*				30.34	27.11-34.23	
C		*				30.62	25.81-33.99	
B			*			31.84	27.80-35.85	
E			*			32.36	28.15-34.30	
						Females		
D	*					26.21	24.25-29.10	< 0.001
A		*				27.44	25.86-29.13	
C			*			27.93	24.36-31.05	
E				*		28.42	26.62-30.49	
B					*	29.13	26.82-39.91	

TABLE 4.—*Continued.*

Group	MRT					Mean	Range	P
						Occipital Depth		
						Males		
D	*					16.30	15.57-17.32	< 0.001
C		*				16.90	15.21-19.02	
A		*				17.36	16.02-19.73	
E			*			18.02	15.60-19.28	
B			*			18.07	15.40-21.27	
						Females		
D	*					15.05	13.94-15.87	< 0.001
C		*				15.83	14.04-17.91	
A			*			16.10	15.07-17.38	
E			*			16.17	15.00-17.29	
B				*		16.87	15.72-18.47	
						Breadth of Rostrum		
						Males		
D	*					11.60	9.80-12.88	< 0.001
A	*	*				11.95	10.75-13.60	
C	*	*				12.10	10.72-13.90	
E		*				12.56	10.53-13.53	
B		*				12.58	10.31-14.72	
						Females		
D	*					9.94	9.27-10.75	< 0.001
A		*				10.38	9.64-11.32	
C		*	*			10.55	9.40-12.25	
E			*			10.63	9.48-12.31	
B				*		11.26	10.16-12.64	
						Length of Rostrum		
						Males		
D	*					21.86	19.38-23.86	< 0.001
C		*				22.98	19.47-26.49	
A			*			24.26	22.22-26.86	
E			*			24.28	20.61-26.25	
B			*			25.02	21.11-28.66	
						Females		
D	*					19.49	17.63-21.78	< 0.001
C		*				20.51	18.40-23.79	
E			*			21.04	19.35-22.71	
A				*		21.67	20.16-27.03	
B					*	22.70	20.16-25.18	

TABLE 4.—*Continued.*

Group	MRT				Mean	Range	P
					Length of Nasals		
					Males		
D	*				18.18	16.20-20.27	< 0.001
C		*			19.00	16.40-21.33	
E			*		19.95	16.99-21.60	
A			*		20.04	17.67-22.24	
B				*	21.02	17.18-24.04	
					Females		
D	*				16.02	13.85-17.25	< 0.001
C		*			17.01	15.40-20.08	
E		*			17.15	15.19-19.29	
A			*		17.75	16.38-19.52	
B				*	18.95	16.99-21.09	
					Interorbital Constriction		
					Males		
D					6.77	6.09-7.13	0.251
A					6.93	6.03-7.74	
C					6.95	6.13-7.95	
B					6.98	6.08-7.95	
E					7.03	6.38-7.49	
					Females		
D	*				6.57	5.91-7.23	0.005
C		*			6.72	5.88-7.92	
E		*			6.74	5.78-7.29	
A		*			6.77	5.53-7.53	
B		*			6.83	5.94-7.70	
					Palatofrontal Depth		
					Males		
D	*				19.25	18.10-20.94	< 0.001
C		*			20.00	17.41-22.14	
A		*			20.55	18.70-23.23	
E			*		21.16	18.01-22.01	
B			*		21.56	18.09-25.05	
					Females		
D	*				17.74	16.48-18.95	< 0.001
C		*			18.63	16.97-20.99	
A		*	*		18.87	15.46-19.93	
E			*		19.09	17.67-20.28	
B				*	20.02	18.25-21.76	

TABLE 4.—*Continued.*

Group	MRT					Mean	Range	P
						Length of Maxillary Toothrow		
						Males		
D	*					9.61	8.97-10.47	< 0.001
C	*					9.75	8.58-10.90	
E	*					9.81	8.57-10.32	
A		*				10.14	9.18-10.99	
B		*				10.36	9.55-11.75	
						Females		
D	*					9.20	8.59-9.84	< 0.001
C		*				9.36	7.78-10.35	
E		*				9.46	8.75-10.28	
A			*			9.76	9.09-10.25	
B				*		9.93	8.77-11.39	
						Length of Palate		
						Males		
D	*					26.79	24.77-29.21	< 0.001
C		*				28.50	25.32-31.34	
A			*			30.26	26.72-34.07	
E			*			30.30	25.65-32.61	
B			*			31.23	27.40-35.12	
						Females		
D	*					24.29	22.52-25.62	< 0.001
C		*				25.88	23.46-30.83	
A			*			27.20	25.51-29.42	
E			*			27.22	25.30-29.63	
B				*		28.59	26.39-31.72	
						Width of Upper Incisor		
						Males		
D	*					3.08	2.69-3.43	< 0.001
C	*					3.21	2.67-3.67	
E	*					3.22	2.84-3.44	
A		*				3.38	2.15-3.78	
B		*				3.43	2.88-3.98	
						Females		
D	*					2.73	2.52-3.00	< 0.001
C		*				2.81	2.47-3.42	
E			*			2.86	2.41-3.33	
A				*		2.96	2.76-3.29	
B					*	3.07	2.70-3.96	

TABLE 4.—*Continued.*

Group	MRT					Mean	Range	P
						Length of Mandibular Toothrow		
						Males		
D	*					8.71	8.12-9.28	< 0.001
C		*				8.92	7.83-9.78	
A			*			9.24	8.48-9.93	
E			*			9.25	8.26-10.29	
B				*		9.51	8.68-10.36	
						Females		
D	*					8.47	7.88-9.01	< 0.001
C		*				8.70	7.75-9.91	
E			*			9.04	8.22-9.83	
A			*			9.07	8.35-10.07	
B				*		9.30	8.14-10.34	
						Depth of Ramus		
						Males		
D	*					17.68	15.43-19.16	< 0.001
A	*	*				17.94	15.91-19.74	
C		*				18.26	16.37-19.61	
E			*			18.80	16.96-19.91	
B			*			18.82	16.75-21.29	
						Females		
D	*					16.21	15.24-17.70	< 0.001
A		*				16.55	15.41-17.35	
C			*			17.05	15.31-18.97	
E				*		17.36	15.48-18.53	
B					*	17.67	16.08-20.20	
						Width of Lower Incisor		
						Males		
D	*					2.95	2.48-3.26	< 0.001
C		*				3.13	2.69-3.52	
E		*				3.14	2.78-3.41	
A		*				3.24	2.78-3.91	
B		*				3.27	2.41-3.95	
						Females		
D	*					2.54	2.33-2.81	< 0.001
C		*				2.65	2.33-3.36	
E		*				2.69	2.37-3.20	
A			*			2.75	2.51-3.02	
B				*		2.88	2.51-3.21	

overlapped were not the same for each character. There was much more overlap in males, indicated by the failure to identify five subsets for any of the characters, and in only three of the characters (condylobasal length, length of nasals, length of mandibular toothrow) were four subsets identified.

The results of my study of geographic variation of *C. castanops* in the United States lead me to recognize nine subspecies. The five morphologically distinct clusters (A-E) and individuals of group 9 are here recognized as separate races. Three peripherally isolated populations are recognized as well. These are described in some detail in the accounts that follow. Subspecies are arranged alphabetically.

Accounts of Subspecies

Cratogeomys castanops
(synonymy under subspecies)

Distribution.—In the United States (Fig. 6), this species occurs from the Arkansas River drainage in eastern Colorado and western Kansas southward through the Oklahoma Panhandle, western Texas, and eastern New Mexico to the Rio Grande; isolated populations are known in the upper Rio Grande Valley (vicinity of Albuquerque, New Mexico), in Maverick County, Texas (vicinity of Eagle Pass), and near Brownsville, Cameron Co., Texas, at the mouth of the Rio Grande. In México, this pocket gopher probably occurs south of the Rio Grande to southern Coahuila and northern Zacatecas, in parts of Nuevo León, and eastward along the south side of the Rio Grande to the Gulf Coast in Tamaulipas (see Davidow-Henry *et al.*, 1989).

Description.—Medium-sized for gophers of the genus *Cratogeomys*; skull without strong platycephalic specializations; squamosals unspecialized, expanded neither medially nor laterally; breadth across zygomata greater than breadth across squamosals; lambdoidal crest convex posteriorly, never sinuous; P4, M1, and M2 lacking posterior enamel plate; outer surface of upper incisors with single median groove; diploid chromosome number 46 (Davidow-Henry *et al.*, 1989).

Comparisons.—From *Cratogeomys merriami*, the only other member of the *castanops* species-group, *C. castanops* differs in being smaller both externally and cranially. *Cratogeomys castanops* shows less cranial and dental specialization than *C. merriami* (Russell, 1968*b*). From the *gymnurus* species-group, to which all other members of the genus are assigned, *castanops* differs in being generally smaller and lacking the strong platycephalic specializations characteristic of the *gymnurus* group (Russell, 1968*b*; Hall, 1981).

Remarks.—*Cratogeomys castanops* is the most wide-spread species of this genus and the only one not restricted to the southern mountainous region of the Mexican Plateau and the Neovolcanic belt (Russell 1968*b*). Given the large geographic distribution and the diverse ecological conditions in which *C. castanops* exists, it is not surprising that it is the most variable of the species in the genus, with 19 currently recognized subspecies (Davidow-Henry *et al.*, 1989). The most subspecies in any of the other species of the genus is seven (Russell, 1968*b*).

Cratogeomys castanops angusticeps Nelson and Goldman

Cratogeomys castanops angusticeps Nelson and Goldman, Proc. Biol. Soc. Washington, 47:139, 1934. Holotype from Eagle Pass, Maverick Co., Texas.

Distribution.—Known only from vicinity of the type locality. See Figures 6 and 7.

Description.—A small, pale race geographically isolated from main distribution of species in the United States; size and cranial dimensions resembling

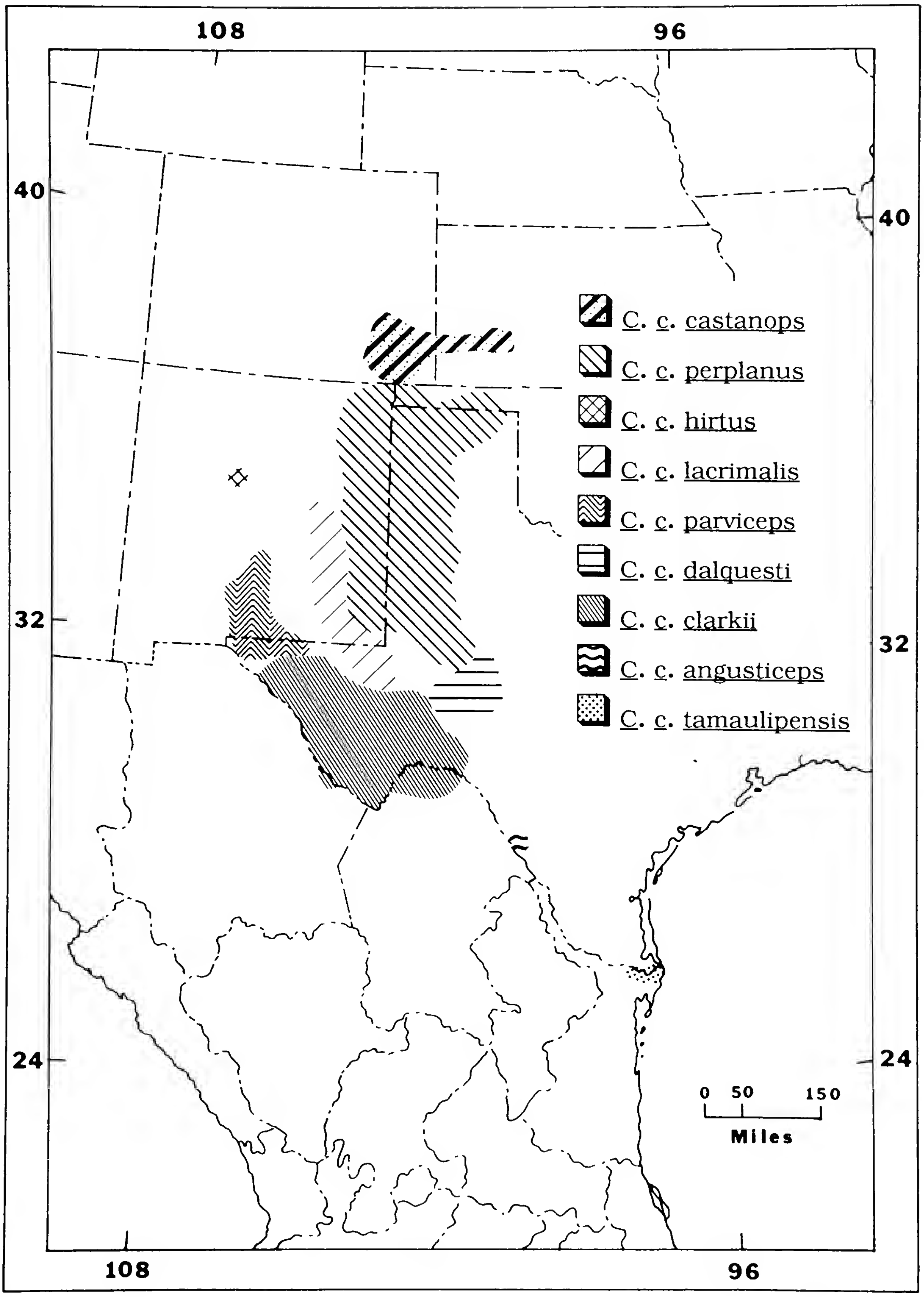

FIG. 6.—Map showing the distribution of the herein recognized subspecies of *C. castanops* in the United States.

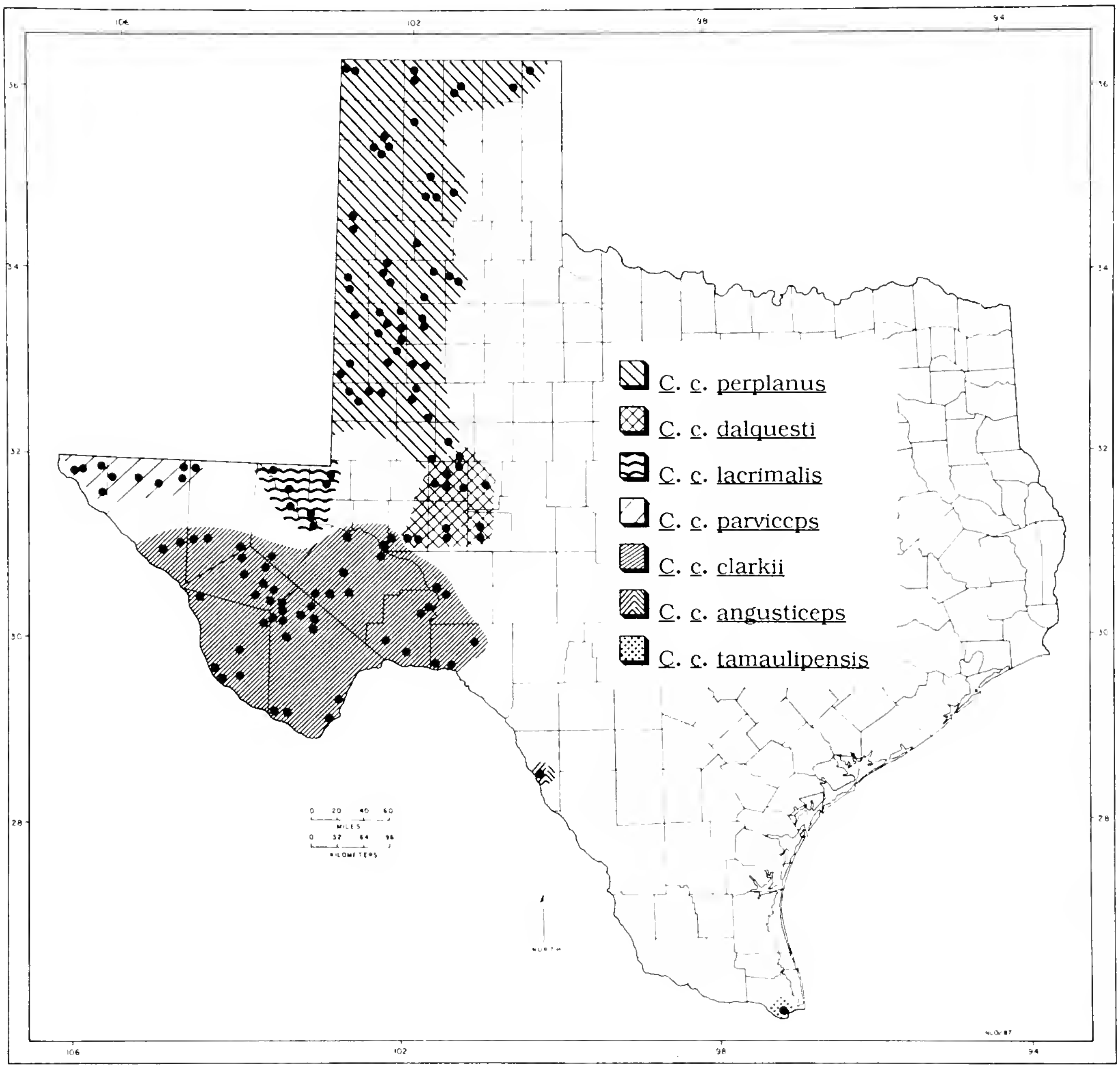

FIG. 7.—Map showing the distributional limits (shading) and localities for specimens examined (dots) of subspecies of *C. castanops* in Texas.

those of *C. c. parviceps* from southwestern New Mexico; means of selected cranial measurements of two adult females and four adult males, respectively, are as follows: condylobasal length, 46.45, 50.27; mastoid breadth, 26.05, 27.89; occipital depth, 15.18, 15.78 (three specimens only); breadth of rostrum, 10.14, 10.76; length of rostrum, 18.85, 21.06 (three specimens only); palatofrontal depth, 17.81, 18.76 (three specimens only); length of mandibular toothrow, 8.80, 8.95.

Comparisons.—From topotypic material of *C. c. tamaulipensis*, *angusticeps* differs in averaging smaller in all cranial dimensions, is paler, and lacks dark postauricular patches. From the population of *tamaulipensis* in Cameron County, Texas, *angusticeps* averages smaller in all cranial measurements except breadth of rostrum, length of maxillary toothrow, and length of mandibular toothrow (the means for these characters are approximately equal for the two races), and specimens of *angusticeps* are much paler (see

account of *tamaulipensis* for details on the Cameron County population). For comparison with *C. c. clarkii*, see account of that subspecies. *C. c. clarkii* and *C. c. tamaulipensis* are the only subspecies occurring near the geographic range of *angusticeps* to the north of the Rio Grande.

Remarks.—The sample size available for *angusticeps* was insufficient for inclusion in multivariate analyses. Russell (1968*b*) referred specimens from northern Terrell County, Texas (west of the Pecos River), to *angusticeps*. Comparison of females from Eagle Pass with a series of females from Independence Creek, Terrell County, using one-way ANOVAs, revealed significant differences in two (length of rostrum and length of mandibular toothrow) of the 15 cranial characters analyzed. These results, combined with the apparent isolated nature of the population in the vicinity of Eagle Pass, warrant its tentative recognition as a distinct subspecies until additional material from the type locality and intervening areas can be obtained. The only gophers presently known from the area between Eagle Pass and the Pecos River are of the genera *Geomys* and *Thomomys*. For details on the Terrell County population, see the account of *C. c. clarkii*.

Specimens examined.—Total of 13 as follows.

TEXAS. *Maverick Co.*: *1 mi. W Seco Mines,* 2; *1 mi. W Eagle Pass,* 2; Eagle Pass, 9 (1 KU, 8 USNM).

Cratogeomys castanops castanops (Baird)

Pseudostoma castanops Baird, Exploration and survey of the valley of the Great Salt Lake of Utah, ... Lippincott, Grambo & Co., Philadelphia, p.313, 1852. Holotype from "Prairie road to Bent's Fort," restricted to near the present town of Las Animas, Bent Co., Colorado by Nelson and Goldman (1934).

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:159, 1895.

Distribution.—Southeastern Colorado and eastward along the north side of the Arkansas River to Ford and Hodgeman counties, Kansas. See Figures 6, 8, and 9.

Description.—Medium-sized race with relatively long, narrow skull; size and cranial dimensions somewhat intermediate between *C. c. perplanus* of Texas and Oklahoma panhandles and *C. c. clarkii* of Trans-Pecos area of Texas; color similar to that of *perplanus* and *C. c. lacrimalis* of southeastern New Mexico, but averaging darker dorsally. See Table 4, group A, for means and ranges of all cranial measurements.

Comparisons.—From *C. c. perplanus*, the only adjacent subspecies (to the south), *castanops* differs in averaging smaller in all cranial dimensions for each sex (see Table 4); it is especially small in mastoid breadth and breadth of rostrum (in both sexes), with only *C. c. parviceps*, *C. c. angusticeps*, and *C. c. tamaulipensis* averaging smaller in these dimensions. From *perplanus*, the subspecies *castanops* also differs in having a greater number of dark-tipped hairs on the dorsum, imparting an overall darker appearance.

Remarks.—Specimens of *C. c. castanops* most closely resemble, in size and color, populations from Glasscock and adjacent counties (group E, Table 4) in west-central Texas than gophers from any other sample. They are,

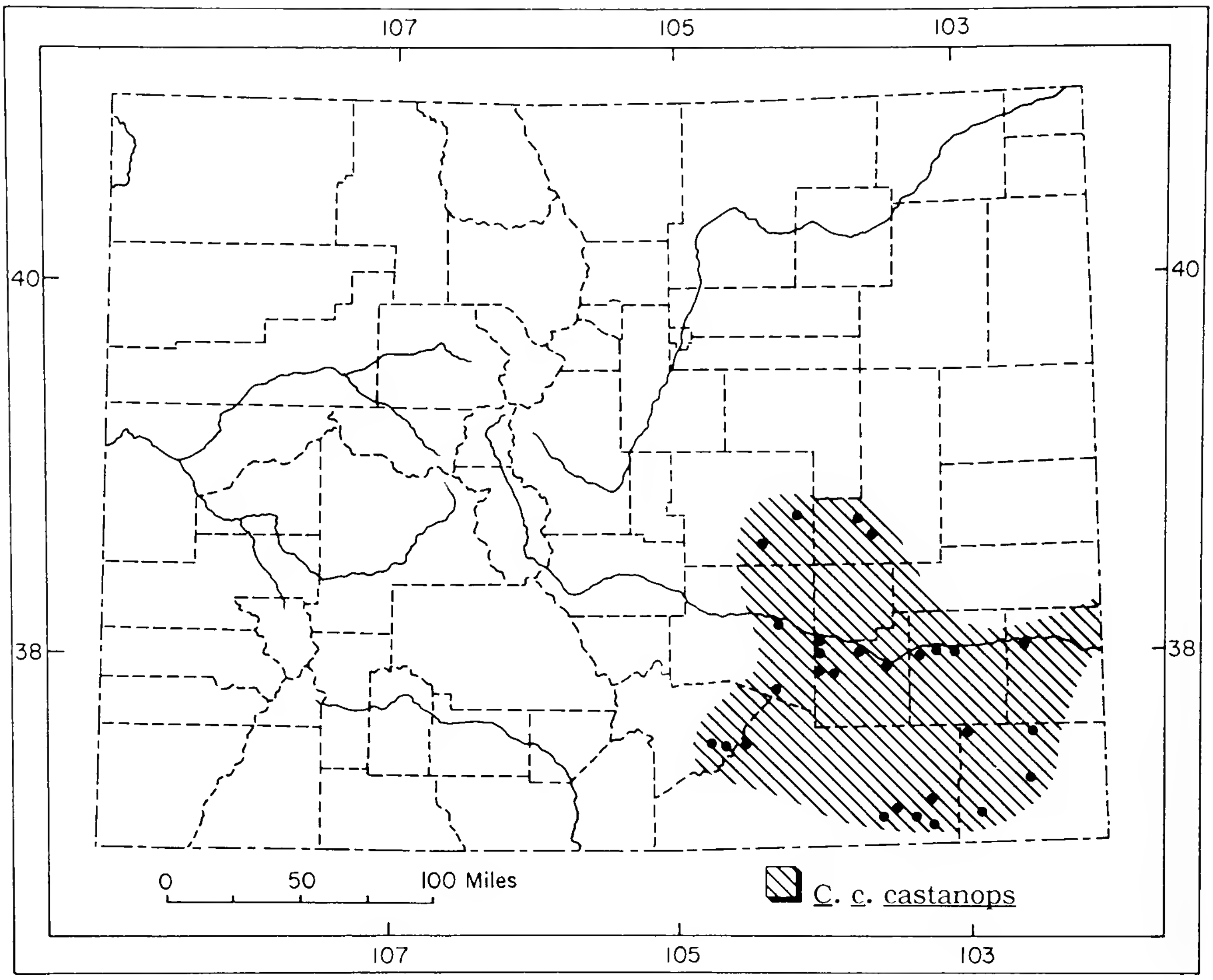

FIG. 8.—Map showing the distributional limits (shading) and localities for specimens examined (dots) of *C. c. castanops* in Colorado.

however, separated from this population by a substantial geographic area that is occupied by a larger race, *C. c. perplanus*.

Gene flow between *perplanus* and *castanops* is evident in samples from southern Baca County, Colorado, and Cimarron County, Oklahoma. Russell (1968*b*) noted that specimens from northwestern Oklahoma appeared to be intermediate between *perplanus* and *castanops* but were best referred to the former. I agree with Russell and assign specimens from that area to *C. c. perplanus*. Specimens from southern Baca County, Colorado, although grading toward the larger *perplanus*, are best referred to *castanops*.

Russell (1968*b*) assigned three specimens from northeastern New Mexico to *castanops*. The current availability of much more material from this area than was available to Russell has facilitated a more thorough analysis. Individuals from Union and Colfax counties, New Mexico, were treated as unknowns in discriminant function analysis (described in section on geographic variation). Only one of these individuals was classified into group A (*castanops*). The remaining individuals (save one) were classified into group B (*perplanus*). Based on these results, specimens from northeastern New Mexico are best assigned to *perplanus* and not to *castanops*.

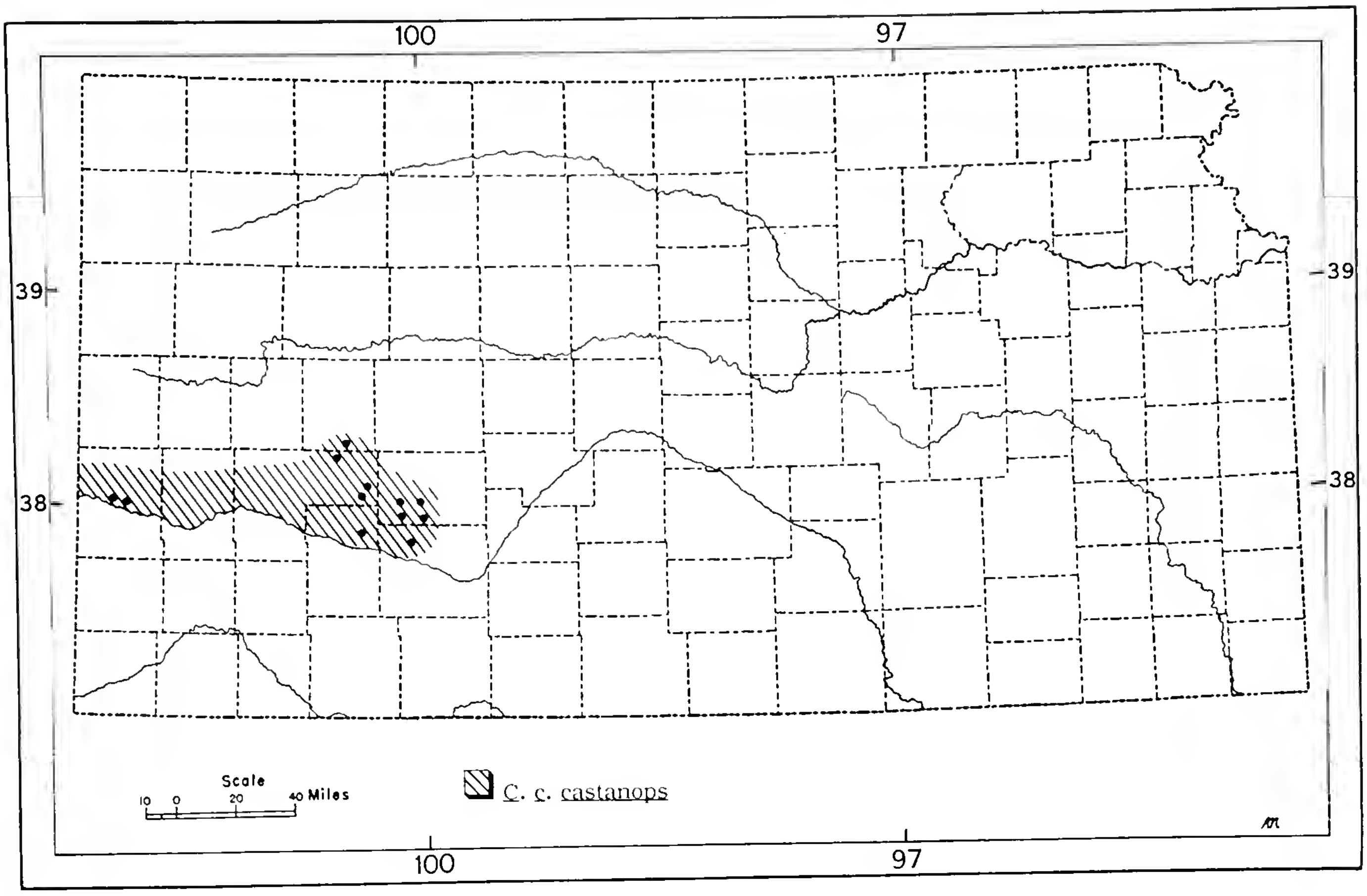

FIG. 9.—Map showing the distributional limits (shading) and localities for specimens examined (dots) of *C. c. castanops* in Kansas.

Specimens examined.—Total of 205 as follows.

COLORADO. *Baca Co.*: Gaume's Ranch, NW corner of Baca County, 2 (UCM); 14 mi. N Springfield, 2 (TCWC); Bear Creek bottom, Springfield, 6 (UCM); 15.25 mi. S, 8 mi. W Pritchett, 1 (MHP); *17 mi. S, 4 mi. W Pritchett,* 3 (MHP); *18 mi. S, 4.25 mi. W Pritchett,* 1 (MHP); *Johnston's Ranch, Monon,* 2 (UCM). *Bent Co.*: Las Animas, 6 (USNM); 2.2 mi. S, 1.5 mi. W John Martin Dam, 2 (MHP); *5.5 mi. S, 1.5 mi. W John Martin Dam,* 1 (MHP); 12 mi. E La Junta [recorded as from Otero County], 2 (KU). *El Paso Co.*: 8 mi. S, 3 mi. W Rush [recorded as from Lincoln County], 1 (MHP); 14 mi. S, 4 mi. W Ellicott, 1 (MHP); *16 mi. S, 2 mi. W Ellicott,* 1 (MHP); *17 mi. S, 4 mi. W Ellicott,* 1 (MHP). *Huerfano Co.*: 3.5 mi. E jct. hwys. I 25 and 10, 1 (MHP); 5.6 mi. S, 7.5 mi. E jct. hwys. I 25 and 10, 1 (MHP). *Las Animas Co.*: 15.4 mi. E jct. hwys. I 25 and 10, 1 (MHP); *7 mi. S, 13.6 mi. E jct. hwys. I 25 and 10 [recorded as from Huerfano County],* 1 (MHP); 1 mi. S, 5.5 mi. E Kim, 1 (MHP); *1 mi. S, 6.5 mi. E Kim,* 1 (MHP); *Tecolote Mesa, 4 mi. S, 2 mi. E Kim,* 1 (MHP); 1.5 mi. W Lone Butte, 1 (MHP); *Mesa de Maya by Lone Butte,* 5 (MHP); *west end of Mesa de Maya,* 6 (MHP); 9 mi. N, 11.5 mi. E Branson, 1 (MHP); *8.5 mi. S, 10.5 mi. W Kim,* 1 (MHP); 8.5 mi. S, 9 mi. W Kim, 10 (MHP); *11.5 mi. S, 7.25 mi. E Kim,* 1 (MHP); *12.25 mi. S, 0.5 mi. E Kim,* 1 (MHP); *12.5 mi. S, 7.5 mi. E Kim,* 1 (MHP); 13 mi. S, 5.5 mi. E Kim, 2 (MHP). *Lincoln Co.*: 11 mi. S, 9 mi. W Punkin Center, 1 (MHP); 10 mi. S, 3 mi. W Karval, 1 (MHP); *12 mi. S, 3 mi. W Karval,* 1 (MHP); *13 mi. S, 4 mi. W Karval,* 1 (MHP). *Otero Co.*: 1 mi. S jct. hwys. 50 and 167, 1 (MHP); 4 mi. W Rocky Ford, 6 (3 KU, 3 TTU); *1.5 mi. E Rocky Ford,* 8 (NMSU); Apishapa River, 7 mi. S, 1 mi. W Fowler [recorded as from Huerfano County], 1 (MSB); La Junta, 3; jct. hwys. 167 and 10, 1 (MHP); 4 mi. N, 6 mi. W Timpas, 2 (MHP); *2 mi. N Timpas,* 1 (MHP). *Prowers Co.*: Lamar, 1; *2 mi. S, 1 mi. E Lamar,* 1. *Pueblo Co.*: 2.7 mi. S, 0.75 mi. E Avondale, 4 (MHP); 14.8 mi. W jct. hwys. 167 and 10, 1 (MHP); *1 mi. N, 8.5 mi. W Goodnight,* 1 (MHP).

KANSAS. *Finney Co.*: 19 mi. S Dighton, 3 (KU); 8.5-9 mi. N, 2 mi. W Kalvesta, 3 (MHP); *8 mi. N, 2.5 mi. W Kalvesta,* 1 (MHP); *6.5 mi. N, 4.5 mi. W Kalvesta,* 4 (MHP); *5 mi. W Kalvesta,* 1 (KU); 3-4 mi. W Kalvesta, 3 (KU). *Ford Co.*: 7.5-8.5 mi. N, 6 mi. E Dodge City, 8 (KU);

Ford County State Lake, 6.5 mi. N, 4 mi. E Dodge City, 30 (KU); *Ford County Lake, 2 mi. N, 1-1.25 mi. W Wright,* 4 (MHP); *5 mi. N, 1 mi. E Dodge City,* 2 (KU); *5 mi. N, 2.5 mi. E Dodge City,* 4 (KU). *Gray Co.*: 10 mi. N, 4.5 mi. E Cimarron, 1 (KU). *Hamilton Co.*: 5 mi. N, 1 mi. W Syracuse, 1 (MHP); *5 mi. N Syracuse,* 1 (KU); *4 mi. N, 1.5 mi. W Syracuse,* 3 (KU); *4 mi. N, 1 mi. W Syracuse,* 5 (MHP); *Hamilton County Lake,* 2 (KU); 3 mi. N, 8 mi. W Syracuse, 2 (MHP); *2.3 mi. N, 0.5 mi. W Syracuse,* 1 (KU); *0.5 mi. NW Syracuse,* 1 (MHP). *Hodgeman Co.*: 12.7 mi. W Jetmore, 1 (KU); *9-10.4 mi. W Jetmore,* 5 (KU); *8.8 mi. W Jetmore,* 1 (KU); 2-2.75 mi. S, 3-3.5 mi. E Jetmore, 10 (MHP); *4 mi. S, 0.5 mi. W Jetmore,* 1 (KU); 10 mi. S, 8 mi. W Jetmore, 1 (KU); 14 mi. S, 6 mi. E Jetmore, 1 (KU). *Lane Co.*: 14 mi. S, 6 mi. E Dighton, 1 (KU); *15 mi. S, 7.5 mi. E Dighton,* 1 (KU).

Cratogeomys castanops clarkii (Baird)

Geomys clarkii Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:332, 1855. Holotype from Presidio del Norte, on the Rio Grande, at or near the present town of Ojinaga, Chihuahua.

Cratogeomys castanops clarkii, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:140, 1934.

Pappogeomys castanops pratensis Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:653, 1968. Holotype from 8 mi. W and 3 mi. S Alpine, Brewster Co., Texas.

Pappogeomys castanops torridus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:665, 1968. Holotype from 3 mi. E Sierra Blanca, Hudspeth Co., Texas.

Distribution.—Southern Trans-Pecos area of Texas from southern Hudspeth County eastward to Crane, Upton, and Val Verde counties, hence southward to the Rio Grande and across the river in the vicinity of Ojinaga, Chihuahua, and adjacent northeastern Coahuila. See Figures 6 and 7.

Description.—Small race characterized by relatively short, wide skull. Skull averaging smaller in all characters than in *C. c. lacrimalis* from northern Pecos Valley (see Table 4, group C, for means and ranges of all cranial measurements). Pelage color in this race extremely variable and seemingly correlated with ecological conditions under which individuals exist; specimens from Davis Mountains, Texas, for example, average much darker than those from lower elevations along the Rio Grande.

Comparisons.—From *C. c. parviceps* and *C. c. angusticeps*, the adjacent races on the west and east, respectively, *clarkii* differs in averaging larger in all cranial dimensions. Specimens of parviceps average much darker than most specimens of *clarkii* although, as noted above, some specimens of the latter from higher elevations are dark in color. Specimens of *angusticeps* typically are much paler than those of *clarkii*. From *C. c. lacrimalis*, the subspecies occurring to the north in the northern Pecos River Valley, *clarkii* differs in averaging smaller for most cranial measurements and has much smaller lacrimal bones. Color in specimens of *clarkii* from lower elevations is similar to that of typical specimens of *lacrimalis*. See account of *C. c. angusticeps* for comparison with specimens from the eastern range of *clarkii*. For comparison with *C. c. perplanus*, see account of that subspecies.

Remarks.—Russell (1968*b*) assigned specimens from the southern Trans-Pecos to four subspecies—*angusticeps*, *clarkii*, *pratensis*, and *torridus*. The latter two are here placed in synonymy under the older name *clarkii*. Specimens from the eastern part of the Trans-Pecos that were allocated to *angusticeps* by Russell are discussed in the account of that subspecies.

Specimens from northern Brewster and Jeff Davis counties, which Russell (1968*b*) assigned to *pratensis*, and specimens from southern Hudspeth County, which he assigned to *torridus*, were found, based upon much larger samples, to be statistically indistinguishable from topotypic material of *clarkii* from the vicinity of Ojinaga, Chihuahua, and from specimens from just north of the Rio Grande near Presidio. Specimens from southern Hudspeth County in, and to the south of, the Sierra Diablo Mountains do average slightly smaller than typical *clarkii*, and this appears to be an area of intergradation between *clarkii* and the smaller *parviceps* to the northwest. These specimens are, however, clearly referable to *clarkii*, whereas specimens from north of the Sierra Diablos in the Culberson Salt Flats are best assigned to the smaller *parviceps*.

Three specimens, housed in the United States National Museum, are recorded from localities east of the Pecos River on the Edwards Plateau—near Ft. Lancaster and Howard Spring, Crockett County, and Juno, Val Verde County. All of these specimens were collected near or before the turn of the century. Recent field work at Ft. Lancaster and Juno in the summers of 1986 and 1987 failed to provide evidence of any extant pocket gopher populations in these areas. In an analysis of the present and past distributions of pocket gophers from cave deposits on the Edwards Plateau, Dalquest and Kilpatrick (1973) reported *Thomomys* and *Geomys*, but not *Cratogeomys*. These three specimens were not included in the multivariate analyses due to skull damage or because they were not of the appropriate age class. Thus, an appraisal of their subspecific status is tentative at best. Because recent efforts to obtain gophers from these areas has failed, and because Dalquest and Kilpatrick (1973) did not find *Cratogeomys* in the fossil material they examined from the Edwards Plateau, it is possible that these specimens represent immigrants from the nearest established populations, which are immediately to the west in the Trans-Pecos area and are here assigned to *clarkii*.

Russell (1968*b*) reported two subspecies from the vicinity of Ojinaga, Chihuahua. I have found that specimens recorded from south of Ojinaga are not assignable to *clarkii* and probably are referable to *C. c. consitus*, a race that occupies northwestern Chihuahua. Additional material from western Chihuahua will be needed to resolve this problem.

Specimens from northern Coahuila tentatively are assigned to *clarkii* on the basis of size. Analysis of additional material from Coahuila and other parts of northern México will be needed before an accurate designation of these specimens can be made.

Specimens examined.—Total of 421 as follows.

CHIHUAHUA. *2 mi. WNW Ojinaga,* 1 (AMNH); *1.5 mi. WNW Ojinaga,* 1 (AMNH); *Ojinaga,* 5 (3 AMNH, 2 KU).

COAHUILA. *17 mi. S Dryden, Texas, on Rio Grande,* 6 (KU); *Villa Acuna,* 5 (KU); *Canyon del Cochino, 16 mi. N, 21 mi. E Piedra Blanca,* 1 (KU); *11 mi. W Hidalgo San Miguel,* 1 (KU).

TEXAS. *Brewster Co.*: 18.6 mi. N, 1.2 mi. E Marathon, 5; 11 mi. N Alpine, 2 (MWSU); *10.2 mi. N Alpine,* 1 (CCSU); *5 mi. N Alpine,* 1 (SRSU); *4 mi. N Alpine,* 1 (SRSU); *11.8 mi. N, 2 mi. E Marathon,* 5; *11.5 mi. N, 2 mi. W Marathon,* 4; *2 mi. NW Alpine,* 1 (SRSU); *3 mi. W Alpine,* 2 (SRSU); Alpine, 10 (6 SRSU, 3 TTU, 1 MWSU); *Sul Ross Ranch,* 1 (SRSU); *Toronto Pass,* 1 (SRSU); *2 mi. S, 6 mi. W Alpine,* 3 (KU); 8 mi. N, 17 mi. W Marathon, 2; *3 mi. S, 10 mi. W Alpine,* 2 (KU); 3 mi. S, 8 mi. W Alpine, 5 (KU); *4 mi. N, 10 mi. W Marathon,* 1 (KU); 10 mi. S Alpine, 1 (SRSU); *12 mi. SE Alpine,* 2 (SRSU); *12 mi. S Alpine,* 1 (SRSU); Marathon County Park, 3 (TAI); *16 mi. S Alpine,* 1 (MWSU); *4.5-5 mi. S Marathon,* 4 (TAI); *6 mi. S Marathon,* 1 (CCSU); 9 mi. S Marathon, 1 (TAI); *22 mi. SE Alpine,* 1 (SRSU); *22 mi. S Alpine,* 2 (SRSU); *15.4 mi. S Marathon,* 2 (CCSU); 26 mi. S Alpine, 1 (UTEP); Black Gap, 3 (TNHC); 8 mi. N Terlingua, 3 (KU); *Terlingua Creek, 4 mi. E Terlingua,* 8 (KU); *4 mi. E Terlingua,* 1 (TCWC); *5-6 mi. S Terlingua,* 3 (KU); Lajitas, 4 (KU); *1 mi. E Lajitas,* 1; *1 mi. SW Boquillas, Rio Grande,* 3 (MVZ); Cottonwood Campground, BBNP, 1 (TCWC); *3 mi. W Rio Grange Village, BBNP,* 1 (TCWC); *8 mi. SW Rio Grande Village, BBNP,* 2 (TCWC); *Big Bend of Rio Grande,* 5 (MVZ); *Brewster County only,* 1 (SRSU). *Crane Co.*: 7 mi. SW McCamey, 1. *Crockett Co.*: Ft. Lancaster, 1 (USNM); 5 mi. S Howard Springs, 1 (USNM). *Culberson Co.*: *25 mi. N Van Horn,* 1 (MWSU); 25 mi. NE Van Horn, 1 (MWSU); 20 mi. N Van Horn, 1 (MWSU); *21 mi. NNE Van Horn,* 1 (MWSU); *6 mi. N Kent,* 1 (MWSU); 6 mi. NW Kent, 1 (MWSU); *1.5 mi. N Kent,* 2 (MWSU). *Hudspeth Co.*: *Bat Cave, Sierra Diablos,* 1 (TCWC); 12 mi. N Allamore, 1 (TCWC); *1 mi. N, 0.5 mi. E Sierra Blanca,* 8 (UIMNH); *3 mi. W Sierra Blanca,* 1 (TCWC); *0.25 mi. W Sierra Blanca,* 4 (UIMNH); Sierra Blanca, 2 (1 UIMNH, 1 TTU); *Methodist Churchyard, Sierra Blanca,* 3 (UIMNH); *2 mi. E Sierra Blanca,* 2 (KU); *3 mi. E Sierra Blanca,* 1 (KU). *Jeff Davis Co.*: 10 mi. S Kent, 1 (MWSU); 4 mi. W Toyavale, 1 (MWSU); *12 mi. S Kent,* 1 (MWSU); *12 mi. S Kent [recorded as from Culberson County],* 1 (MWSU); *13 mi. S Kent,* 1 (MWSU); *15 mi. S Kent [recorded as from Culberson County],* 2 (MWSU); 20 mi. SSE Kent, 1 (MWSU); *11 mi. NE McDonald Observatory,* 1 (MWSU); *10 mi. NE McDonald Observatory,* 1 (MWSU); *3.6 mi. NNW Nunn Hill, Davis Mts.,* 1 (MWSU); *26 mi. NW Ft. Davis,* 1 (MWSU); 16 mi. N Ft. Davis, 3 (TCWC); *Madera Canyon only,* 4 (TCWC); *Frazier Canyon, 10 mi. N Ft. Davis,* 2; *Limpia Canyon, 10 mi. NE Ft. Davis,* 1; *4.8 mi. WSW McDonald Observatory,* 1 (MWSU); 9 mi. E Mt. Livermore, 3 (TCWC); *7.5 mi. E Mt. Livermore,* 3 (TCWC); *Limpia Canyon, 9.5 mi. NE Ft. Davis,* 1; *9 mi. N Ft. Davis,* 1 (CCSU); *Limpia Canyon, 8.8-9.2 mi. NE Ft. Davis,* 30; *Limpia Canyon, 8 mi. NE Ft. Davis,* 1; *7.5 mi. NW Ft. Davis,* 1 (MWSU); *Limpia Canyon, 6.7 mi. NE Ft. Davis,* 2; *Limpia Canyon, 4 mi. NW Ft. Davis,* 3; *Limpia Canyon, 3 mi. NW Ft. Davis,* 2; *Limpia Canyon only,* 2 (ASU); *2 mi. NW Ft. Davis,* 1 (MWSU); *Limpia Creek by Davis Mts. State Park,* 1; 1 mi. N Ft. Davis, 8 (TCWC); 9 mi. W Ft. Davis, 5 (TCWC); *5 mi. W Ft. Davis,* 12 (TCWC); *1 mi. SE Ft. Davis,* 1; *2 mi. S Ft. Davis,* 2; *3.8 mi. SE Ft. Davis,* 1; *4.1 mi. SE Ft. Davis,* 1; *5 mi. S Ft. Davis,* 1 (SRSU); *15 mi. NW Alpine,* 3 (SRSU); *12.6 mi. N Alpine [recorded as from Brewster County],* 1 (CCSU). *Pecos Co.*: 20 mi. N Ft. Stockton, 1 (MWSU); 2 mi. N Girvin, 3; Ft. Stockton, 4 (KU); *30 mi. SE Ft. Stockton,* 3 (SRSU); 35 mi. SE Ft. Stockton, 1 (SRSU); 33 mi. S Ft. Stockton, 2; 21.2 mi. N, 1.5 mi. W Marathon, 2. *Presidio Co.*: *11 mi. W Valentine,* 10 (TNHC); 9 mi. W Valentine, 4 (CCSU); 9 mi. NE Marfa on hwy. 67, 2; *2 mi. S Paisano,* 10 (TCWC); *36 mi. SE Marfa,* 2; 37 mi. S Marfa, 2 (TCWC); *1 mi. W Plata,* 1 (MWSU); 63 mi. S Marfa, 1 (TNHC); *3 mi. NW Presidio,* 2 (AMNH); *2 mi. NW Presidio,* 1 (TCWC); *Presidio,* 8 (KU); 0.5 mi. S Presidio, 1 (TCWC); *1 mi. S, 2 mi. E Presidio,* 1 (KU); *1 mi. S, 4 mi. E Presidio,* 2 (KU); 3 mi. S, 6 mi. E Presidio, 1 (KU); *7 mi. ESE Presidio,* 2 (AMNH). *Reeves Co.*: 3 mi. WNW Toyavale, 3 (MWSU); *4 mi. W Toyavale,* 4 (MWSU). *Terrell Co.*: *15-16 mi. S Sheffield,* 10 (9 TNHC, 1 TTU); *hwy. crossing at Independence Creek,* 1 (SRSU); 16 mi. S, 6 mi. E Sheffield, 11; *19-20 mi. S Sheffield,* 20 (TNHC); 24 mi. S Sheffield, 1; *1 mi. N Sanderson,* 4 (MWSU); 2 mi. E Sanderson, 14 (12 TCWC, 2 KU); *3 mi. W Dryden,* 9 (KU); 2 mi. W Dryden, 5 (KU); *1 mi. W Dryden,* 2 (KU). *Upton Co.*: 4 mi. N, 5 mi. W McCamey, 1. *Val Verde Co.*: 20 mi. E Juno, 1 (USNM); Samuels, 19 mi. W Langtry, 1 (USNM); 8 mi. S Langtry, 1 (USNM); *between Pecos and Rio Grande rivers,* 1 (USNM).

Cratogeomys castanops dalquesti, new subspecies

Holotype.—Female, adult, skin and skull, The Museum, Texas Tech University no. 44458, from 1 mi. N and 4 mi. W Sterling City, Sterling Co., Texas; obtained on 10 June 1986 by Robert R. Hollander, original no. 1506. External and cranial measurements of the holotype are as follows: total length, 268; length of tail vertebrae, 68; length of hind foot, 38; length of ear, 7; weight, 256 grams; condylobasal length, 51.79; zygomatic breadth, 32.88; mastoid breadth, 28.86; occipital depth, 17.01; breadth of rostrum, 10.59; length of rostrum, 21.64; length of nasals, 16.97; least interorbital constriction, 6.62; palatofrontal depth, 19.84; length of maxillary toothrow, 9.02; length of palate, 28.50; width of upper incisor, 2.98; length of mandibular toothrow, 9.17; depth of ramus, 17.28; width of lower incisor, 2.57.

Distribution.—West-central Texas north of the Edwards Plateau and south of the Llano Estacado from the upper Concho River Valley in Sterling and Glasscock counties westward to eastern Upton County. See Figures 6 and 7.

Description.—Relatively large race having a long skull with relatively short rostrum and nasals, short toothrows relative to lengths of skull and palate, and large and conspicuous lacrimals; see Table 4, group E, for means and ranges of all cranial measurements. Color similar to *castanops* in having a large number of dark-tipped hairs on the dorsum imparting a dark, grizzled appearance.

Comparisons.—From female *C. c. perplanus*, the subspecies occurring to the north, female *dalquesti* differ in averaging smaller in all cranial dimensions. Males of *dalquesti* average smaller than males of *perplanus* in all cranial dimensions save zygomatic breadth, mastoid breadth, and interorbital constriction, which are similar. In both sexes, *dalquesti* averages darker dorsally than *perplanus*. The most distinguishing characteristic separating *dalquesti* from *perplanus* is the size and shape of the lacrimal bones. This qualitative character was not included in the multivariate analysis but is depicted in Figure 10. In this character, *dalquesti* demonstrates a closer relationship to *C. c. lacrimalis* and *C. c. clarkii* than with either *perplanus* or *castanops*.

From *C. c. clarkii*, the race to the southwest, *dalquesti* differs in averaging larger in all cranial characters and in being much darker in color (with the exception of specimens of *clarkii* from the Davis Mountains). The lacrimal bone of *dalquesti* is larger than that of *clarkii*.

C. c. dalquesti is geographically isolated from *C. c. lacrimalis* of the northern Pecos River Valley of Texas and eastern New Mexico (see Fig. 7), but the two taxa closely resemble each other. From *lacrimalis*, *dalquesti* differs in averaging darker in color and having smaller lacrimal bones that protrude less into the orbit (see Fig. 10).

Remarks.—In a study of geographic variation in *Cratogeomys castanops* on the Llano Estacado of Texas and New Mexico, Dowler and Genoways (1979) included specimens from Glasscock County in one of their samples. They

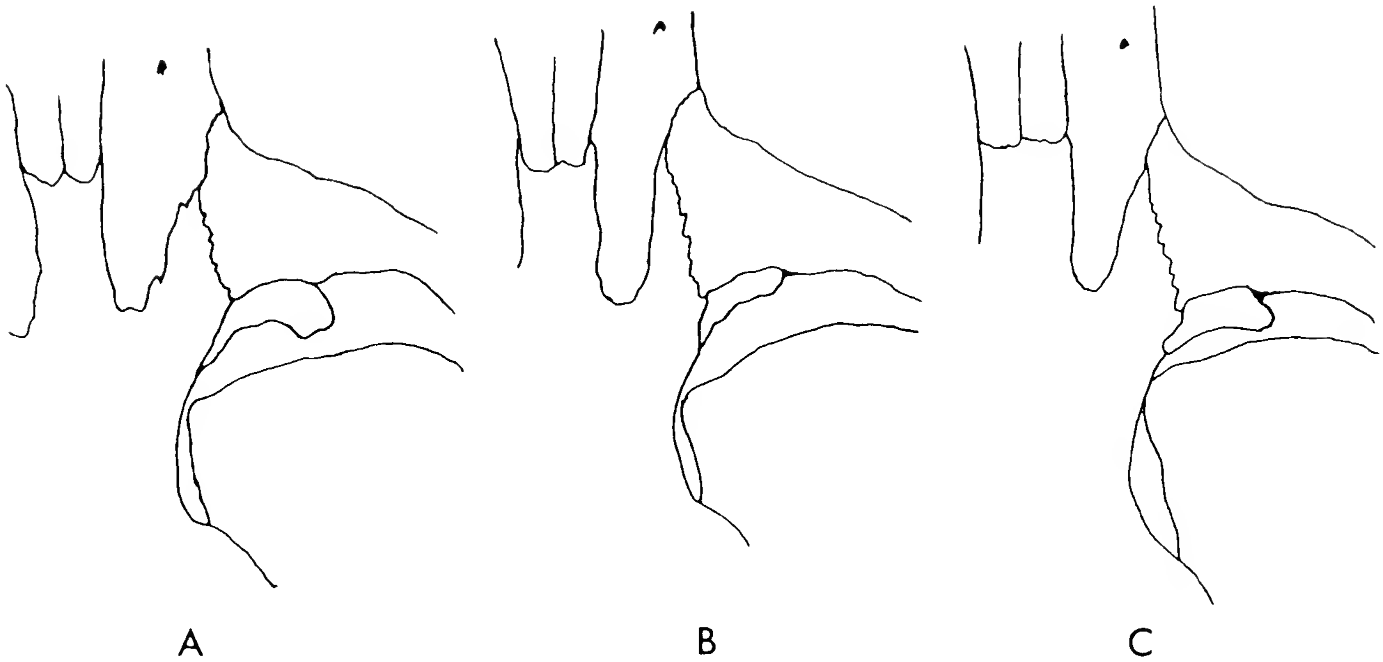

FIG. 10.—Partial view of the crania depicting the size, shape, and relative position of the lacrimal bone of A) *C. c. lacrimalis*, adult female (TTU 45535) from 2 mi. N, 5 mi. E Mentone, Loving Co., Texas; B) *C. c. perplanus*, adult female (TTU 26407) from 1.8 mi. N Littlefield, Lamb Co., Texas; and C) *C. c. dalquesti*, adult female (TTU 26047) from 2 mi S, 12 mi. W Garden City, Glasscock Co., Texas.

noted that gophers in this sample (which they labeled 12) were distinctly smaller than specimens to the north and west and did not fit the pattern of clinal variation they observed. Other samples from the Llano indicated a north-south increase in size. They suggested that the Glasscock County sample might represent intergrades between *C. c. perplanus* and the smaller *C. c. angusticeps* to the south. Most of the specimens examined by them, along with many additional specimens from adjacent areas, are here recognized as distinct and the name *C. c. dalquesti* proposed to represent them. This population is geographically isolated from *angusticeps* by the Edwards Plateau and shows no affinities with that race.

C. c. dalquesti may come into contact with *C. c. perplanus* along the southeastern edge of the Llano. A specimen from Big Spring is clearly referable to *perplanus* and probably is from above the caprock on the north side of that city, whereas specimens from Glasscock County to the south of Big Spring are clearly assignable to *dalquesti* and are from below the caprock. There is no evidence of hybridization in this area and it appears that the caprock may be a substantial barrier to movement of *C. castanops* and prevents these two races from coming into contact. A similar situation is present to the west in the area of Stanton. A specimen labeled as from Stanton and on top of the caprock is referable to *perplanus*, whereas those from southeast of Stanton in Glasscock County and off the caprock are referable to *dalquesti*.

C. c. dalquesti is separated from *C. c. clarkii* in western Upton County by a fingerlike extension of the Edwards Plateau escarpment and a population of *Thomomys bottae* (Hollander *et al.*, 1987). This extension of the escarpment

extends in a northwestern direction almost to the Monahans Sandhills in eastern Crane County, and is referred to locally as King and Castle mountains. Specimens from west of the escarpment are clearly assignable to *clarkii*, whereas specimens from east of the escarpment (vicinity of Rankin) are clearly referable to *dalquesti*. There is no evidence of intergradation in this area between *clarkii* and *dalquesti*. It appears that the population of *Thomomys* that occurs near and to the east of McCamey or the Edwards escarpment, or some combination of both, provide a substantial barrier to gene flow between *clarkii* and *dalquesti* in this area.

Individuals of *dalquesti* show many morphological affinities with specimens of *C. c. lacrimalis* from the Pecos River Valley of western Texas and eastern New Mexico. Cranially, these races are similar although typical specimens of *dalquesti* are much darker in color than are those typical of *lacrimalis*. The two races are geographically separated by the Llano Estacado (which is occupied by *C. c. perplanus*) and the vast area of the Monahans Sandhills to the south and west of the Llano (the only gopher reported from this sandy tract is *Geomys bursarius knoxjonesi*—Hollander *et al.*, 1987). Extensive field work in this area of Texas has produced no populations of *Cratogeomys* that could link these two subspecies. Until additional material from intermediate areas is available to suggest otherwise, the two appear to be geographically isolated.

Etymology.—It gives me great pleasure to name this subspecies in honor of Walter W. Dalquest of Midwestern State University. Dr. Dalquest has made numerous contributions to our knowledge of mammalian faunas of Texas, especially Pleistocene faunas. Through his efforts and those of his students, the largest series of this taxon available for study is housed in the mammal collection of Midwestern State University.

Specimens examined.—Total of 95 as follows.

TEXAS. *Glasscock Co.*: 20 mi. SSE Big Spring, 1 (MWSU); 15 mi. N Garden City, 2 (MWSU); *14.5 mi. N Garden City,* 1 (MWSU); *12.7 mi. N Garden City,* 1 (MWSU); *12 mi. N Garden City*, 1 (MWSU); *11 mi. N Garden City,* 1 (MWSU); *10.9 mi. N Garden City,* 1 (MWSU); *10.7 mi. N Garden City,* 1 (MWSU); *9.6-9.7 mi. N Garden City,* 5 (MWSU); *6 mi. N Garden City,* 2 (ASU); *5.7 mi. N Garden City,* 2 (MWSU); *5.1 mi. N Garden City,* 1 (MWSU); *5 mi. N Garden City,* 1 (MWSU); *4.7 mi. N Garden City,* 1 (MWSU); *3.3 mi. N Garden City,* 1 (MWSU); *2 mi. N, 13.7 mi. W Garden City,* 1; *2 mi. N, 13 mi. W Garden City,* 1; *1.8-1.9 mi. N, 12.7-12.8 mi. W Garden City,* 5; *1.4 mi. N, 13.3 mi. W Garden City,* 1; 19-20 mi. S Stanton, 3; *2.6 mi. S jct. hwys. 137 and 158 on 137,* 1 (ASU); *1.1 mi. N Garden City,* 1 (MWSU); 0.9 mi. N Garden City, 1 (MWSU); *0.6 mi. N Garden City,* 2 (MWSU); *10.4-10.6 mi. W Garden City,* 3 (MWSU); *0.8 mi. W Garden City,* 1 (MWSU); *0.5 mi. S, 13 mi. W Garden City,* 1; *0.7 mi. S, 12.4 mi. W Garden City,* 2; *1 mi. S, 12.5 mi. W Garden City,* 1; *1.3 mi. S, 12 mi. W Garden City,* 2; *2 mi. S, 12 mi. W Garden City,* 2; *2.4 mi. S, 11.8-12 mi. W Garden City,* 4; *0.2 mi. W Sterling County line on hwy. 158,* 1 (ASU); *Glasscock County only,* 4 (NMSU). *Howard Co.*: 11.2 mi. S Big Spring, 1 (MWSU); *13 mi. SSE Big Spring,* 1 (MWSU). *Irion Co.*: 10.5 mi. N jct. hwys. 163 and 2469, 1 (ASU); *9.2 mi. N jct. hwys. 163 and 2469,* 1 (ASU); *22 mi. N Barnhart,* 1; *8.2 mi. N jct. hwys. 163 and 2469,* 2 (ASU); 3 mi. N jct. hwys. 163 and 2469, 1 (ASU). *Reagan Co.*: 30 mi. S Garden City, 1; *19.1 mi. N Big Lake,* 1 (ASU); *Centralia Draw, 18.2 mi. N Big Lake,* 1 (ASU); 3 mi. NE Stiles, 1. *Sterling Co.*: 7.3 mi. N jct. hwy. 163 and U.S. hwy. 87, 1 (MWSU); *6.7 mi. N jct. hwy. 163 and U.S. hwy. 87,* 1 (MWSU); *6 mi. N jct. hwy. 163 and U.S. hwy. 87,* 1 (MWSU); *9.7 mi. NW Sterling City,* 1 (MWSU); *7.5 mi. NW Sterling City,* 1

(MWSU); *2 mi. N jct. hwy. 163 and U.S. hwy. 87,* 1 (MWSU); *6.4 mi. NW Sterling City,* 2 (MWSU); *1.5 mi. N jct. hwy. 163 and U.S. hwy. 87,* 1 (MWSU); *5.5-5.6 mi. NW Sterling City,* 4 (MWSU); *0.7 mi. N jct. hwy. 163 and U.S. hwy. 87,* 2 (MWSU); *4 mi. NW Sterling City,* 2 (MWSU); *1 mi. N, 4 mi. W Sterling City,* 1; *23.7 mi. E Garden City,* 1 (ASU); 25 mi. E Garden City, 1 (ASU). *Upton Co.*: Rankin, 2; *2 mi. E Rankin,* 1; 8 mi. E Rankin, 1.

Cratogeomys castanops hirtus Nelson and Goldman

Cratogeomys castanops hirtus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:138, 1934. Holotype from Albuquerque, Bernalillo Co., New Mexico.

Distribution.—Known only from vicinity of the type locality. See Figures 6 and 11.

Description.—Russell (1968*b*) described this race as small for the species, but he included specimens of *C. c. parviceps* from the Tularosa Basin in the description. Nelson and Goldman (1934), in the original description of *hirtus*, stated it was a dark-colored subspecies closely allied to *C. c. lacrimalis* (of the Pecos Valley), and limited it to the upper Rio Grande Valley. Selected cranial measurements of an adult female topotype are as follows: condylobasal length, 47.31; zygomatic breadth, 29.84; breadth of rostrum, 10.66; palatofrontal depth, 18.18; length of maxillary toothrow, 10.04.

Comparisons.—Only one adult specimen of this subspecies was examined by me. Russell (1968*b*) included some specimens here referred to *parviceps* within this race and described it as being small. The adult female and a subadult female (the third specimen was a young individual) I examined both are larger than the average of *parviceps* examined for most cranial characters and approximate the size of *C. c. clarkii* of the Trans-Pecos.

Remarks.—This taxon is poorly known and peripherally isolated from the main body of the species in the United States. Specimens from southwestern New Mexico that were assigned to this race by Russell (1968*b*) are separated from the type locality by the large expanse of the Jornado del Muerto, an area from which no pocket gophers of any kind have been reported. Specimens from Rhodes Pass and El Paso are clearly referable to *parviceps* (see account of that subspecies for details). Of the four specimens of this subspecies (as here defined) that are known, three were obtained in 1894. The fourth was not collected until 1962, and none has been acquired since that time. Until additional material from the vicinity of the type locality is available for study, an accurate description of *hirtus* cannot be written nor can its status be ascertained with confidence.

Specimens examined.—Total of 3 as follows.
NEW MEXICO. *Bernalillo Co.*: Albuquerque, 2 (USNM); *South Valley, Albuquerque,* 1 (MSB).

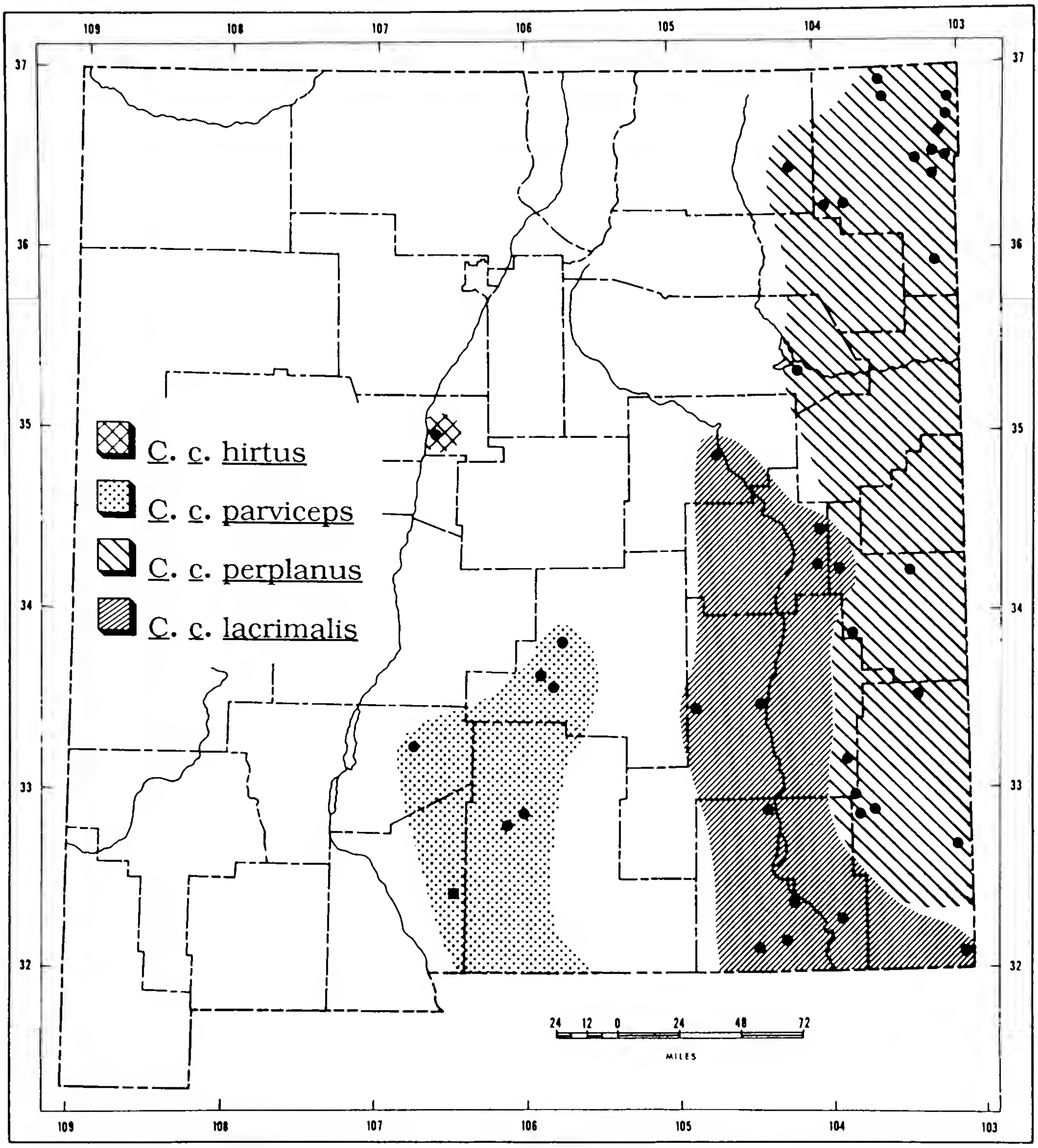

FIG. 11.—Map showing the distributional limits (shading) and localities for specimens examined (dots) of subspecies of *C. castanops* in New Mexico.

Cratogeomys castanops lacrimalis Nelson and Goldman

Cratogeomys castanops lacrimalis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:137, 1934. Holotype from Roswell, Chaves Co., New Mexico.

Distribution.—Pecos River Valley west of the Llano Estacado from Guadalupe County, New Mexico, southwardly to Reeves, Ward, and Winkler counties, Texas. See Figures 6, 7, and 11.

Description.—Medium to large-sized subspecies characterized by large lacrimal bones that project posteriorly into the orbit (see Fig. 10). Size slightly smaller than in *C. c. perplanus* and slightly larger than in *C. c. castanops* and *C. c. dalquesti*.

Comparisons.—From *C. c. perplanus*, the race occurring on the Llano Estacado to the east, *lacrimalis* differs in being smaller in most cranial dimensions and in having enlarged lacrimals. Size and shape of the lacrimal of *C. c. lacrimalis*, *C. c. perplanus*, and *C. c. dalquesti* are compared in Figure 10. For comparisons with *C. c. clarkii*, *C. c. dalquesti*, and *C. c. parviceps*, see accounts of those subspecies.

Remarks.—Russell (1968*b*) assigned specimens from the Pecos Valley of eastern New Mexico and northwestern Texas to *perplanus*, placing *lacrimalis* in synonymy. In discriminant function analysis, individuals here referred to *lacrimalis* (group 9, Fig. 3) were treated as unknowns so as to ascertain if they more closely resembled morphologically one of the *a priori* clusters (A-E). These specimens were classified almost equally into *C. c. castanops* (cluster A), *C. c. perplanus* (cluster B), *C. c. clarkii* (cluster C), and *C. c. dalquesti* (cluster E), indicating no stronger alliance with any one than the others. Specimens from above the western escarpment of the Llano Estacado (which is not as distinct as the eastern escarpment) were almost always classified as *perplanus*. These results and the characteristic size and shape of the lacrimal bone (discussed above) indicated the need for resurrecting the name *lacrimalis* for this distinct race inhabiting the Pecos Valley.

There is an area of integration between *lacrimalis* and *perplanus* in the vicinity of Maljamar, Lea Co., New Mexico. This area is just above the caprock and, based on the size of gophers and variation in the shape of the lacrimal bone, gene flow between the two races takes place in this area. All specimens from there, however, are assignable to *perplanus*.

Specimens examined.—Total of 106 as follows.

NEW MEXICO. *Chaves Co.*: 20 mi. W Roswell, 1 (NMSU); *2 mi. E Roswell,* 1 (MSB); Roswell and 0.5 mi. S, 12 (11 KU, 1 ENMU). *De Baca Co.*: 2.7-3.4 mi. S, 0.3 mi. E Taiban, 4; *5.8 mi. S, 0.3 mi. E Taiban,* 2; 13 mi. S, 0.75 mi. W Taiban, 2. *Eddy Co.*: Artesia, 7 (NMSU); 3 mi. NW Carlsbad, 1 (MSB); *Carlsbad,* 16 (3 KU, 1 MHP, 12 NMSU); *1-2 mi. E Carlsbad,* 10 (KU); 6 mi. S, 22 mi. E Carlsbad, 1 (ENMU); 5 mi. S, 1 mi. E Black River Village, 1 (KU); 2 mi. S, 1 mi. W White City, 1 (KU); *Rattlesnake Springs, CCNP,* 2 (KU); *0.8 mi. N, 8.5 mi. E jct. hwy. 128 and 31 on 128,* 2 (MSB). *Guadulupe Co.*: 1 mi. S Santa Rosa, 4; *Catfish Falls, Los Esteros Lake Site,* 2 (MSB). *Lea Co.*: 2 mi. S, 7 mi. E Jal, 1 (ENMU). *Roosevelt Co.*: 15.3-15.4 mi. W Floyd, 4; *11.8-13 mi. W Floyd,* 17.

TEXAS. *Loving Co.*: Red Bluff Lake Dam, 1 (SRSU); *2 mi. N, 5 mi. E Mentone,* 1; *2 mi. W Mentone,* 1; 1 mi. W Mentone, 3; *0.5 mi. W Mentone,* 1. *Reeves Co.*: 15 mi. N Pecos, 2 (SRSU); 5 mi. S, 10 mi. E Pecos, 1. *Ward Co.*: 2 mi. W Barstow, 2. *Winkler Co.*: 5.5 mi. W Kermit, 1; *Kermit,* 2; 2.6 mi. N Wink, 1; *1.25 mi. N, 3 mi. W Wink,* 1.

Cratogeomys castanops parviceps (Russell)

Pappogeomys castanops parviceps Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:673, 1968. Holotype from 18 mi. SW Alamogordo, Otero Co., New Mexico.

C[*ratogeomys*]. *c*[*astanops*]. *parviceps*, Jones, Jones, and Schmidly, Occas. Papers Mus., Texas Tech Univ., 119:11, 1988.

Distribution.—Tulorosa Basin of southwestern New Mexico and western Texas. See Figures 6, 7, and 11.

Description.—A small subspecies with a short, narrow skull; pelage typically dark both dorsally and ventrally, but some individuals from lower elevations are paler. See Table 4, group D, for means and ranges of cranial measurements.

Comparisons.—From *C. c. lacrimalis* of the Pecos Valley to the east, *parviceps* differs in being much smaller in all cranial dimensions, and specimens of *parviceps* are typically much darker than those of *lacrimalis*. For comparisons with *C. c. clarkii* and *C. c. hirtus*, see accounts of those subspecies.

Remarks.—Russell (1968*b*) allocated *C. c. parviceps* to the *subnubilus* subspecies-group of *C. castanops*, a subspecies-group that he restricted primarily to México; *parviceps* was the only member found in the United States. This subspecies-group was characterized by small size, both externally and cranially. Although *parviceps* is one of the smallest races in the United States, it is no smaller than *C. c. angusticeps* and is similar in size to *C. c. tamaulipensis*. These latter two races were allocated to the larger *excellsus* subspecies-group by Russell (1968*b*). In a recent study of the louse-host associations with *C. castanops*, Hellenthal and Price (1976) redefined the distribution of Russell's *excellsus*-group and *subnubilus*-group based on the distribution of species of *Geomydoecus*. Their new distribution corresponded with the suggested distribution of Berry and Baker (1972), and later Lee and Baker (1987), of the two groups of gophers based on chromosome number. All these data suggest that the *subnubilus*-group (which Lee and Baker, 1987, believed is specifically distinct from *C. castanops*) should be restricted to the southern Mexican Plateau, and that *parviceps* should be placed in the *excellsus*-group. The results of the analyses of morphological data in this study support these conclusions.

Russell (1968*b*) also reported an area of sympatry between *parviceps* and specimens of *C. c. perplanus* (here assigned to *C. c. lacrimalis*) in the Guadalupe Mountains of western Texas. In a study of the mammals of this area, Genoways *et al.* (1979) reported only *C. c. parviceps*. They addressed the problem of sympatry between the two races reported by Russell (1968*b*) and stated that they never obtained specimens of *C. castanops* from east of the mountains despite extensive efforts to do so. All specimens available to me from this area are clearly referable to *parviceps*; *lacrimalis* seems to be restricted to lower elevations in the Pecos Valley.

Specimens examined.—Total of 144 as follows.

NEW MEXICO. *Donna Anna Co.*: 1.8 mi. N, 11.7 mi. E Organ, 1 (NMSU); *Parker Lake, E of Organ Mts.*, 4 (USNM). *Lincoln Co.*: Ancho, 1 (USNM); 1.4 mi. N, 0.8 mi. W Carrizozo, 1 (NMSU); *1.2 mi. N, 1 mi. W Carrizozo,* 3 (NMSU); *1.2 mi. W Carrizozo,* 5 (UTEP); 0.5 mi. S, 2.7 mi. E Carrizozo, 6 (NMSU); *0.4 mi. S, 1.6 mi. W Paton Mt.*, 2 (NMSU). *Otero Co.*: 5 mi. S Alamogordo, 1; *5 mi. SW Alamogordo,* 1 (KU); *Holloman AFB golf course,* 3 (NMSU); 1.5 mi. N, 1.9 mi. W White Sands National Monument HQ, 2 (NMSU); *White Sands National Monument,* 3; *18 mi. SW Alamogordo,* 6 (2 MSB, 3 KU, 1 MVZ); *T20S, R12E, N 1/2 sec. 9,* 1 (UTEP). *Sierra Co.*: 3.9 mi. S, 13.2 mi. W Salinas Peak, 33 (NMSU); *4.9 mi. S, 12.1 mi. W Salinas Peak,* 13 (NMSU); *4.2 mi. N, 17.7 mi. E Engle,* 1 (NMSU); *6.2 mi. S, 10.2 mi. W Salinas Peak,* 1 (NMSU); *8.5 mi. S, 11.2 mi. W Salinas Peak,* 1 (NMSU); *8.5 mi. S, 11.8 mi. W Salinas Peak,* 2 (NMSU); *Rhodes Pass, San Andres Mts.*, 5 (UTEP).

TEXAS. *Culberson Co.*: 7 mi. N Pine Springs, GMNP, 1 (TCWC); *Scott Canyon, GMNP,* 2 (TCWC); *Pine Springs Canyon, GMNP,* 1 (TCWC); *Delaware Springs,* 1 (SRSU); *2 mi. SSE El Capitan,* 1 (MWSU). *El Paso Co.*: *1.1 mi. N, 1.7 mi. E Hueco Tanks State Park,* 1 (UTEP); south side of Hueco Tanks State Park, 4 (1 SRSU, 3 UTEP); *Hueco Bolson,* 1 (UTEP); *0.7-0.8 mi. N hwy. 180/62 on FR 2775,* 6 (UTEP); 11 mi. N, 12.5 mi. E El Paso on hwy. 180/62, 1 (UTEP); *11 mi. N, 13 mi. E El Paso on hwy. 180/62,* 1 (UTEP); *10 mi. N, 11 mi. E El Paso,* 1 (UTEP); *15.2 mi. E El Paso on hwy. 180/62,* 1 (UTEP); *0.7 mi. S Carlsbad hwy. and 13.2 mi. E Cinema Park [= El Paso],* 1 (UTEP); *2 mi. S Carlsbad hwy. and 14 mi. E Cinema Park [= El Paso],* 1 (UTEP); El Paso, 1 (UTEP); *Municipal golf course, El Paso,* 1 (MVZ); 9.3-9.4 mi. NE hwy. I 10 on Fabens-Carlsbad Rd., 11 (UTEP); *El Paso County only,* 1 (UTEP). *Hudspeth Co.*: Lewis Well, GMNP, 1; *1 3/8 mi. N, 4.25 mi. W Guadalupe Peak, GMNP,* 2; 3.5 mi. E Salt Flat, [recorded as from Culberson County] 1 (SRSU); southern Hueco Mts., 3 mi. E Horizon Lake, 1 (UTEP); 24 mi. W Cornudas, 1; *3.6 mi. W Cornudas,* 1; *2 mi. W Cornudas,* 1; 1 mi. E Cornudas, 1.

Cratogeomys castanops perplanus Nelson and Goldman

Cratogeomys castanops perplanus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:136, 1934. Holotype from Tascosa, 3000 ft., Oldham Co., Texas.

Pappogeomys castanops simulans Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:656, 1968. Holotype from 17 mi. SE Washburn, Armstrong Co., Texas.

Distribution.—Northeastern New Mexico eastward through the Oklahoma Panhandle, and on the High Plains of the Texas Panhandle southwardly on the Llano Estacado at least as far as Martin County, Texas, and central Lea County, New Mexico. See Figures 6, 7, 11, and 12.

Description.—Largest subspecies of *C. castanops* in the United States; color about as in *C. c. lacrimalis*; lacrimal bone small and articulating more with maxilla than with frontal (Fig. 10). See Table 4, group B, for means and ranges of the cranial measurements.

Comparisons.—From *C. c. clarkii,* of the Trans-Pecos, *perplanus* is geographically isolated by the Monahans Sandhills and the escarpment of the Llano Estacado. For comparisons with the subspecies *castanops*, *dalquesti*, and *lacrimalis,* see accounts of those taxa.

Remarks.—Dowler and Genoways (1979) allocated specimens referred by Russell (1968*b*) to *C. c. simulans* to *C. c. perplanus* and placed the name *simulans* in synonymy. Russell (1968*b*) reported that specimens of *simulans* occurred east of the caprock (Llano Estacado escarpment) in the Texas Panhandle and that this was the barrier between *simulans* and *perplanus*. Dowler and Genoways (1979), however, documented that no specimens of

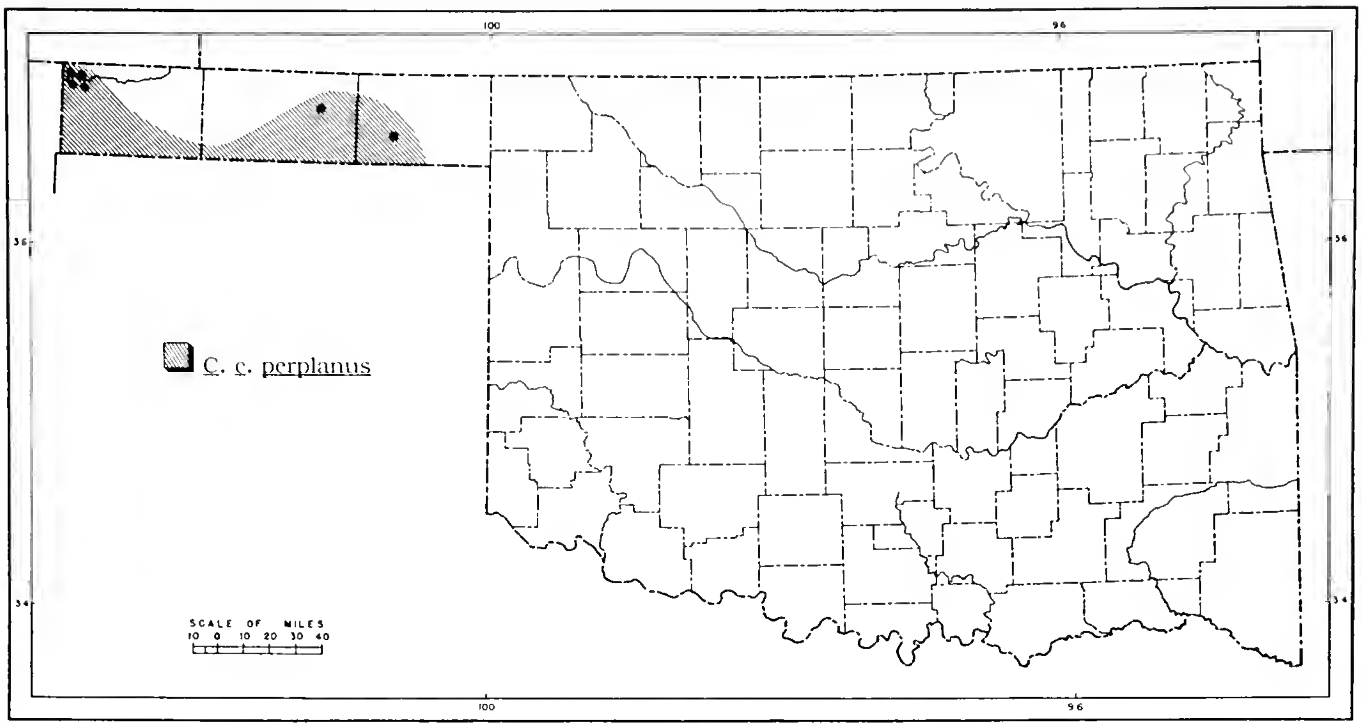

FIG. 12.—Map showing the distributional limits (shading) and localities for specimens examined (dots) of *C. c. perplanus* in Oklahoma.

C. castanops were known from east of the caprock, and demonstrated, with the much larger sample available to them, that *simulans* and *perplanus* were indistinct at the subspecific level. My findings agree with theirs.

For details on situations where *perplanus* comes into contact with the subspecies *castanops*, *dalquesti*, and *lacrimalis*, see accounts of those taxa.

Specimens examined.—Total of 654 as follows.

NEW MEXICO. *Chaves Co.*: 5.7 mi. N, 27.7 mi. E Hagerman, 1; *33 mi. E Lake Arthur,* 1; *7 mi. N Maljamar,* 4 (KU). *Colfax Co.*: Chico Springs, 2 (USNM). *Lea Co.*: *4.2 mi. W Crossroads,* 1; 2.7-3.5 mi. W Crossroads, 10; *0.7-1 mi. W Crossroads,* 9; 7.2 mi. N, 2.1 mi. W Maljamar, 2; *5.8 mi. N, 1.5 mi. W Maljamar,* 1; *3.5 mi. N, 0.5 mi. W Maljamar,* 3; *2 mi. N, 3 mi. E Maljamar,* 1; 0.6-1.4 mi. N, 0.5-0.6 mi. E Maljamar, 8; 11 mi. E Maljamar, 1; 3 mi. N Hobbs, 4 (KU). *Roosevelt Co.*: Portales, 1 (ENMU); 0.9 mi. S, 1.3 mi. W Kenna, 1. *San Miguel Co.*: 1 mi. S, 2 mi. W Conchas Dam, 5 (KU). *Union Co.*: Pepper Ranch, 9 mi. N, 34 mi. E Folsom, 1 (ENMU); 29.5 mi. N, 0.9 mi. E Mt. Dora, 1 (ENMU); 6 mi. N, 2.6 mi. E Moses, 1 (ENMU); *3.3 mi. N, 2.2 mi. E Moses,* 1 (ENMU); 3 mi. ENE Seneca, 1 (MWSU); Rabbit Ears Mt., 2 (MWSU); 6.5 mi. N, 3.5 mi. E Clayton, 3 (ENMU); 4.1 mi. N, 9 mi. E Clayton, 3 (ENMU); *2.9 mi. N, 1.7 mi. W Clayton,* 1 (ENMU); *1.1 mi. N, 2.3 mi. W Clayton,* 1 (ENMU); 6.6 mi. S, 3.5 mi. E Mt. Dora, 2 (ENMU); *0.5 mi. E Clayton Lake,* 1 (ENMU); 9.7 mi. S Clayton, 2 (ENMU); 4.5 mi. N, 5.2 mi. E Pasamonte, 1 (ENMU); 1.3 mi. E Gladstone, 2 (ENMU); *2.2 mi. E Gladstone,* 1 (ENMU); 0.6 mi. N, 0.5 mi. W Amistad, 1 (ENMU).

OKLAHOMA. *Beaver Co.*: 4 mi. E Elmwood Post Office, 4 (OSU). *Cimarron Co.*: 8.3 mi. N, 0.6 mi. E Kenton, 1 (MHP); *7 mi. N Kenton,* 7 (KU); *5 mi. N, 0.5 mi. W Kenton,* 3 (ENMU); *5 mi. N Kenton,* 1 (MWSU); *4.5 mi. NNW Kenton,* 2 (MWSU); *4.4 mi. N, 4 mi. W Kenton,* 1 (OMNH); 4.1 mi. N, 8.2 mi. E Kenton, 1 (MHP); *4 mi. N Kenton,* 3 (MWSU); *3 mi. N, 1 mi. E Kenton,* 3; *near Kenton,* 1 (OMNH); *1 mi. E Kenton,* 3; *0.4 mi. S, 3.4 mi. E Kenton,* 3 (ENMU); 1.5 mi. S, 3 mi. E Kenton, 3; *4-4.1 km. SE Kenton,* 11 (OMNH); *3 mi. S, 3 mi. E Kenton,* 1; *5 mi. E Kenton,* 1 (MHP); *3.75 mi. S, 9.25 mi. E Kenton,* 1 (OMNH); 25 mi. NW Boise City, 1 (OMNH). *Texas Co.*: Railroad right-of-way just W Hooker, 5 (OSU).

TEXAS. *Armstrong Co.*: 8 mi. S, 7 mi. W Claude, 1 (KU); *17 mi. SE Washburn,* 8 (TNHC). *Bailey Co.*: 5.5 mi. S, 2 mi. W Needmore, 1; 22 mi. S Muleshoe, 2. *Cochran Co.*: 0.5 mi. N, 2.7 mi. W Morton, 1; *1.2 mi. S, 1.5 mi. E Morton,* 1. *Dallam Co.*: 12 mi. E Texline, 1; 1.7 mi. S, 0.3 mi. W Texline, 1 (NMSU); *2.4 mi. S, 0.3 mi. W Texline,* 1 (NMSU). *Dawson Co.*: 11.1 mi. N, 3 mi. E Lamesa, 3 (MHP); *11.1 mi. N, 4.3 mi. E Lamesa,* 5 (MHP); *Lamesa,* 1 (MWSU); *10 mi. E Lamesa,* 2 (TNHC); *2.2 mi. S, 0.3 mi. E Lamesa,* 1; 2.3 mi. S Lamesa, 7; *2.8 mi. S, 0.6 mi. E Lamesa,* 2; *2.9 mi. S Lamesa,* 4; *3.3 mi. S, 4 mi. E Lamesa,* 5; *4.6 mi. S, 4.3 mi. E Lamesa,* 1; *5-5.2 mi. S, 4.5-5 mi. E Lamesa,* 6; *6 mi. S, 5.7 mi. E Lamesa,* 6; *6.8 mi. S, 1.3 mi. E Lamesa,* 4; *22 mi. SW Lamesa,* 5 (ASU); 1 mi. NNW Ackerly, 1. *Deaf Smith Co.*: *1 mi. N, 18.3 mi. W Hereford,* 15; *1 mi. N, 17.9 mi. W Hereford,* 4; 1 mi. N, 16.4 mi. W Hereford, 7; *1 mi. N, 15.5 mi. W Hereford,* 1. *Floyd Co.*: *0.4 mi. N, 1.8 mi. W Aiken,* 1; 0.4 mi. N, 1.2 mi. W Aiken, 12; 0.4 mi. N, 1.8 mi. W Lockney, 7; *1.5 mi. W Lockney,* 1; *1.3 mi. W Lockney,* 2; *1 mi. W Lockney,* 5; *0.5 mi. W Lockney,* 1. *Gaines Co.*: *4.4 mi. N, 9.3 mi. W Seminole,* 19; 4.4 mi. N, 7.6 mi. W Seminole, 1; *4.4 mi. N, 6.2-6.6 mi. W Seminole,* 5; 0.8 mi. N, 6.3 mi. E Seminole, 1; 0.8 mi. S, 15 mi. E Seminole, 1; 3 mi. SW Seminole, 1. *Hale Co.*: Plainview, 7 (2 MWSU, 5 TTU); *3 mi. S Plainview,* 2; 3 mi. N, 1 mi. E Abernathy, 5 (MHP). *Hansford Co.*: 5 mi. SW Gruver, 2 (MWSU); *6 mi. S, 3 mi. W Gruver,* 1 (KU); 11 mi. SSW Gruver, 1 (MWSU). *Hartley Co.*: 1 mi. N, 8 mi. W Channing, 1. *Hockley Co.*: 6 mi. SE Anton, 6 (4 ASU, 2 TTU); Yellow House Ranch, 1 (SRSU); *1 mi. N, 4.3 mi. W Levelland,* 3; *1 mi. N, 1 mi. W Levelland,* 1; *0.5 mi. N, 3.2-3.5 mi. W Levelland,* 20; *0.5 mi. N Levelland,* 1; Levelland, 1; 2 mi. E Smyer, 2 (ASU); *3 mi. SW Levelland,* 1; *2 mi. S, 3.8 mi. W Levelland,* 2; *2 mi. S, 2.8 mi. W Levelland,* 7; *7 mi. S Levelland,* 1; 0.5 mi. W Sundown, 1; Ropesville, 3. *Howard Co.*: Big Spring, 1 (USNM); *1 mi. from jct. I 10 and Cauble Rd.,* 1 (ASU). *Lamb Co.*: 1.3 mi. E Earth, 1; 4.8 mi. S, 0.3 mi. W Earth, 5; 1.8 mi. N Littlefield, 3; *1.5 mi. N, 1.5 mi. W Littlefield,* 4; *Littlefield,* 1 (TNHC); *0.5 mi. S, 3 mi. W Littlefield,* 5; *1.5 mi. S, 1.8 mi. E Littlefield,* 5. *Lipscomb Co.*: 5 mi. S Booker, 4 (WTSU). *Lubbock Co.*: 10-10.1 mi. N Lubbock, *7; 7.5-8.5 mi. N Lubbock,* 101 (1 MWSU, 100 TTU); *Airport, 5-6.3 mi. N Lubbock,* 26 (1 MWSU, 25 TTU); *5 mi. NW Lubbock,* 1 (ASU); *4.4 mi. N, 2.5 mi. E Lubbock,* 1; *Mackenzie Park, 2-3 mi. NE Lubbock,* 7; *1.3 mi. N, 2.3 mi. W Lubbock,* 1; *1 mi. N, 10 mi. W Lubbock,* 1; *6.5-7 mi. W Lubbock,* 4 (1 MHP, 3 TTU); *5-5.5 mi. W Lubbock,* 13; *4 mi. W Lubbock,* 1; Lubbock, 29 (1 TAI, 24 TTU, 4 MWSU); *6 mi. E Lubbock,* 1 (MWSU); *1 mi. S, 7 mi. W Lubbock,* 2; *2.5 mi. S, 4.5 mi. E Lubbock,* 1; *4 mi. S, 5.7 mi. E Lubbock,* 1. *Lynn Co.*: 1 mi. E West Point, 1; *Tahoka,* 1 (MWSU); 3 mi. S Tahoka, 1 (MHP). *Martin Co.*: Stanton, 1 (USNM). *Moore Co.*: 3 mi. S Dumas, 2. *Ochiltree Co.*: *11 mi. S, 4 mi. E Perryton,* 1; 12 mi. S, 9 mi. E Perryton, 9. *Oldham Co.*: 3 mi. W Boy's Ranch Headquarters, 1; *Tascosa,* 2 (USNM); 17 mi. N, 1 mi. W Adrian, 1; 20.2 mi. NW Vega, 2 (SRSU). *Parmer Co.*: 0.5 mi. N Friona, 1 (MHP). *Potter Co.*: 3.5 mi. W Amarillo, 1; *2 mi. E Amarillo,* 2 (TCWC). *Randall Co.*: 1 mi. N, 4.8 mi. E Canyon, 4; *0.2 mi. N, 6.5 mi. E Canyon,* 2; *2-2.6 mi. E Canyon,* 7; *3 mi. E Canyon,* 6; *4.8 mi. E Canyon,* 1; *5 mi. S Canyon,* 1; Palo Duro Canyon, 1 (TWC). *Sherman Co.*: Stratford, 3; 8 mi. S, 2 mi. E Stratford, 1. *Swisher Co.*: 4.5 mi. S County Line (probably the small country store referred to locally as County Line approximately 19 mi. W Tulia), 1. *Terry Co.*: 1.7 mi. S, 0.5 mi. W Meadow, 1; 11.2 mi. W Brownfield, 1; *6 mi. W Brownfield,* 3; *Brownfield golf course,* 4; *near Brownfield,* 5. *Yoakum Co.*: 1.6 mi. E Plains, 1; 10.7 mi. W Plains, 1.

Cratogeomys castanops tamaulipensis Nelson and Goldman

Cratogeomys castanops tamaulipensis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:141, 1934. Holotype from Matamoros, Tamaulipas.

Distribution.—Recorded from the United States only from the vicinity of Brownsville, Cameron Co., Texas; known also along the lower reaches of the Rio Grande in Tamaulipas. See Figures 6 and 7.

Description.—Small subspecies that approaches the size of *C. c. clarkii* and *C. c. castanops*; characterized by dark postauricular patches. Geographically

isolated from other *Cratogeomys* in the United States by the lower Rio Grande Valley, which is occupied by *Geomys personatus*.

Comparisons.—For comparison with *C. c. angusticeps*, see account of that subspecies.

Remarks.—Cleveland (1977) first reported *C. castanops* from southern Texas and noted that the nearest record of occurrence for the species was from across the Rio Grande in Tamaulipas. He observed numerous burrows southeast of Brownsville in 1976, but stated that no burrows were observed at the same site in 1972. This suggests the possibility of recent invasion by these gophers from the south side of the river even though Hickmann (1977) reported that *Cratogeomys* was the poorest swimmer among the three genera of pocket gophers in the United States. Cleveland did not assign his specimens to subspecies. These and additional material from the same area were compared by me with topotypic material of *tamaulipensis* using one-way ANOVAs (sample size was too small for multivariate tests). The results of these univariate tests indicated no significant differences between the two populations for any of 15 cranial characters. Thus, until additional material is available for study, this population is best referred to *tamaulipensis*.

Specimens examined.—Total of 19 as follows.

TAMAULIPAS. *3 mi. SE Reynosa,* 3 (KU); *Matamoros,* 8 (5 USNM, 3 TTU).

TEXAS. *Cameron Co.*: 5 mi. SE Brownsville, 1 (TWC); *6 mi. SE Brownsville,* 1 (TWC); *7.2 mi. SE Brownsville,* 6 (TAI).

Discussion

Nine subspecies of *C. castanops* are here recognized as occurring in the United States. They are differentiated primarily by cranial size and some qualitative cranial characters. They can be divided into four general size categories based on cranial dimensions: smallest subspecies—*parviceps* and *angusticeps*; small subspecies—*clarkii, hirtus*, and *tamaulipensis*; medium-sized subspecies—*castanops*, *dalquesti*, and *lacrimalis*; large subspecies—*perplanus*. None of the subspecies in any single size category is geographically adjacent to any of the others in that same category. It seems that size parameters that distinguish the races here recognized are morphological expressions of adaptations to particular environmental conditions under which the several populations exist. For example, the largest subspecies, *perplanus*, occupies the Llano Estacado and the High Plains regions of Texas, Oklahoma, and New Mexico. This area is characterized by relatively deep, rock-free soils (in most areas) as indicated by the vast amount of agriculture in the region. These conditions may favor the increased size of these gophers in that area. Particular conditions under which the other races exist, however, are not as readily apparent because most do not occur in as homogeneous an environment as does *perplanus*.

Biogeography and Evolution

The earliest fossil representative of a lineage that includes *C. castanops* is a species of the closely related genus *Pappogeomys* from late Pliocene deposits in southern Arizona (Russell, 1968*a*). The presumed origin of *castanops* was prior to Rancholabrean times, probably in the late Blancan (Russell, 1968*b*), although it was noted that the first known fossils of *Cratogeomys* were from late Pleistocene (Wisconsin) deposits. Russell (1968*a*) pointed out that although one species (*castanops*) of *Pappogeomys* (including *Cratogeomys* as a subgenus) ranged into the southwestern United States in the late Pleistocene, the genus was essentially Mexican in distribution. Current fossil records of *C. castanops* (discussed in the introductory remarks and beyond) indicate that the species had occupied most of its current range in the United States by late Pleistocene and early Holocene times.

The interpopulation structure of *C. castanops* was discussed in detail by Russell (1969). Using the then available fossil material as evidence for a southern distribution of the species, he proposed three disjunct populations of *castanops* during the pluvial maximum of the Wisconsin (Russell, 1969:fig. 15). These populations gave rise to the "subspecies clusters" and subspecies-groups that he described (Russell, 1968*b*; 1969). The availability of additional extant and fossil material (north of his proposed Pleistocene distribution) of *C. castanops* from the United States demands a reevaluation of Russell's conclusions.

Harris (1985) discussed fossil remains of *C. castanops* from several stadial sites in the Guadalupe Mountains of southeastern New Mexico and western

Texas. He demonstrated that populations of *castanops* were maintained much farther north during the Pleistocene than envisioned by Russell (1968*a*; 1968*b*; 1969). The occurrence of *C. castanops* in the southwestern United states during the Pleistocene negates Russell's (1969) hypothesized post-Wisconsin reinvasion of this region. Although I agree with Russell on the Mexican origin of the species, it is obvious that it has occupied most of its range in the United States, with perhaps the exception of the northern part, since at least mid-Pleistocene times.

The validity of the two subspecies-groups (as described by Russell, 1968*b*) recently has been questioned (Berry and Baker, 1972; Hellenthal and Price, 1976; Lee and Baker, 1987). Berry and Baker (1972) described two distinct cytotypes of *C. castanops*—a southern population with a diploid number of 42, and a northern population with a diploid number of 46. The distribution of these chromosomal forms did not correspond to the distribution of Russell's (1968*b*) subspecies-groups. Hellenthal and Price (1976) described the distribution of species of *Geomydoecus* (lice parasitic on *Cratogeomys*) that corresponded with the distribution of the two cytotypes of *castanops* described by Berry and Baker (1972). Lee and Baker (1987) analyzed the G-banded chromosomes of the two cytotypes and suggested that the two were specifically distinct.

Russell (1968*b*) placed *C. c. parviceps* from southwestern New Mexico in his *subnubilus* subspecies-group of small-sized gophers. This was the only race of *castanops* outside of México that he relegated to that group. Russell (1968*b*) distinguished the two subspecies-groups primarily on size of cranial dimensions. As has been pointed out in the preceding accounts, *C. c. parviceps* averages no smaller than do some of the other races of *castanops* in the United States, all of which Russell placed in the larger *excellsus* subspecies-group. The results of my study, based on morphology, together with the results of the previously mentioned studies based on chromosomes and lice, suggest that the subspecies-groups as described by Russell (1968*b*: fig. 3) have little basis in fact and thus there is no reason for their continued recognition.

Most of the subspecies recognized and discussed in the preceding accounts closely resemble geographically adjacent races. Limited interbreeding may occur between those races not separated by a biogeographic barrier. For example, *C. c. castanops* and *C. c. perplanus* appear to intergrade in the area where Colorado, Oklahoma, and New Mexico share a common border; *C. c. perplanus* and *C. c. lacrimalis* seem to interbreed in the area of western Lea County, New Mexico, where the western escarpment of the Llano Estacado does not appear to be of sufficient magnitude to preclude gene flow. However, along the southeastern edge of the Llano, in Howard and Martin counties, Texas, the distributions of *C. c. perplanus* and *C. c. dalquesti* approach each other geographically but there is no apparent gene flow between the two races, one on the Llano Estacado and one to the south of

it. A similar situation exists between *C. c. dalquesti* and *C. c. clarkii* in the area of Upton and Crane counties in west-central Texas. Here, a northwestern extension of the Edwards Plateau escarpment (which is occupied by another gopher, *Thomomys bottae*) separates the two races and there is no apparent interbreeding. *Cratogeomys castanops dalquesti* is geographically isolated from the closely related *C. c. lacrimalis* by the Monahans Sandhills, which are occupied by *Geomys bursarius*, and the southern Llano Estacado, which is occupied by *C. c. perplanus*, and no interbreeding can take place in the absence of geographic contact. The Sierra Diablo Mountains of western Texas seem to limit gene flow between *C. c. clarkii* and *C. c. parviceps* to a degree, but hybridization does appear to occur. Although there is no apparent barrier to gene flow between *C. c. clarkii* and *C. c. lacrimalis* in the northern Pecos Valley of Texas, I have been unable to detect intergradation there. Additional material may reveal that hybridization does in fact take place.

The three remaining subspecies of *C. castanops* in the United States are geographically isolated from the main population and from each other. *Cratogeomys castanops hirtus* is restricted to the northern Rio Grande Valley in the vicinity of Albuquerque, New Mexico. So few specimens of this taxon are known that an accurate determination of its status is not possible at this time. The other two races, *C. c. angusticeps* and *C. c. tamaulipensis*, are isolated along the lower Rio Grande; *C. c. angusticeps* is restricted to the vicinity of Eagle Pass, Maverick County, Texas, whereas *C. c. tamaulipensis* occurs in Tamaulipas and in the United States only in the vicinity of Brownsville, Cameron County, Texas.

The historical center of distribution of *C. castanops* in the United States seems to be Trans-Pecos Texas and southeastern New Mexico. This is the area where some of the oldest fossils of the species have been found (Harris, 1985). The subspecies that occur in this area today are *C. c. clarkii* and *C. c. lacrimalis*, which closely resemble each other. Assuming that this area was the geographic center of the species in the United States in late Pleistocene times, the current distribution of the subspecies may have proceeded as follows.

A population extended up the Pecos River Valley (currently *C. c. lacrimalis*) and from there gophers migrated onto the Llano Estacado, moved up the Llano to the Canadian River Valley and onward into southeastern Colorado, finally occupying the Arkansas River Valley. They also crossed the Canadian onto the High Plains of the Texas and Oklahoma panhandles. Populations on the Llano Estacado and adjacent High Plains, in the presence of optimal ecological conditions, differentiated into the large gopher here recognized as *C. c. perplanus*. The population in southeastern Colorado, in the presence of less favorable conditions and possibly more intergeneric competition, differentiated much in the same way as did *perplanus* but maintained a smaller size. This population, here recognized as *C. c. castanops*, moved down the Arkansas River into Kansas as well.

The original stock also migrated to the south and east. Gophers that became isolated east of the Pecos River, between the Llano Estacado and the Edwards Plateau, are now geographically separated from those in the Pecos Valley of southeastern New Mexico (yet the two populations closely resemble each other), and are here recognized as *C. c. dalquesti*. The southern population differentiated by becoming smaller, probably as an adaptation to the more xeric conditions of the Chihuahuan Desert, and is here referred as *C. c. clarkii*. This subspecies probably has recently crossed the Rio Grande into México (Russell, 1968*b*). A western extension of this population migrated into the Tularosa Basin of southwestern New Mexico and western Texas and differentiated into one of the smallest races in the United States, *C. c. parviceps*.

The paucity of specimens from the isolated population in the northern Rio Grande Valley make an accurate determination of its affinities difficult. It may represent a relic of an earlier northward surge of gophers up the Rio Grande Valley. In any event, it represents a distinctive race (*C. c. hirtus*) that, based on size alone, probably is more closely related to *C. c. lacrimalis* of the Pecos River Valley to the east. The populations of gophers along the southern Rio Grande (*C. c. angusticeps* and *C. c. tamaulipensis*), because of their isolation from the main populations in the United States, probably are more closely related to, and originated from (by breaching the Rio Grande), populations of *C. castanops* in México as suggested by Russell (1969).

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Address of author: *The Museum and Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409.* Present address: *Department of Biology, Sul Ross State University, Alpine, TX 79832.*
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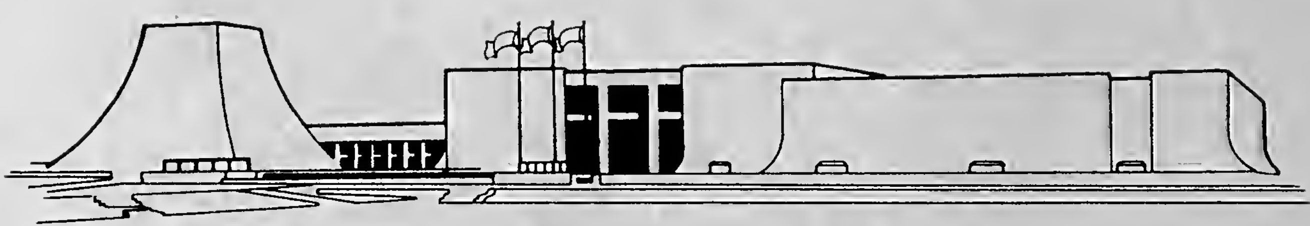

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